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THE EPIZOOTIOLOGY OF AVIAN HEMATOZOA IN BIRDS FROM COMOX BURN, VANCOUVER ISLAND WITH EMPHASIS ON BLUE GROUSE, *LEUCOCYTOZOON*, AND ITS VECTORS

BY

Ⓒ NORMAN A. WILLIAMS

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "The Epizootiology of Avian Hematozoa in Birds from Comox Burn, Vancouver Island, with emphasis on Blue Grouse, *Leucocytozoon*, and its vectors" submitted by Norman A. Williams in partial fulfillment of the requirements for the degree of Master of Science.

ABSTRACT

The prevalence and intensity of avian blood parasite infections (*Leucocytozoon, Haemoproteus, Trypanosoma,* and microfilariae) in blue grouse *(Dendragapus obscurus fulginosus* (Ridgway)*)* and twenty-eight species of non-tetraonid birds from Comox Burn, Vancouver Island were investigated. Blue grouse possessed significantly higher prevalences (80 percent) than their non-tetraonid counterparts (35 percent). This difference is predicated on the basis of host preference by, or host availability to, vectors. Infections of *L. bonasae* (79 percent) were more common than with *H. canachites* (57 percent), *T. avium* (45 percent), or microfilariae (27 percent). Although blue grouse 38 km north harbor infections of *Plasmodium*, birds from Comox Burn were not infected with this parasite genus. Non-tetraonid birds harbored infections of *Leucocytozoon* (21 percent) more often than of *Haemoproteus* (13 percent), *Trypanosoma* (9 percent), or microfilariae (1 percent).

The acquisition of *L. bonasae* by blue grouse chicks occurred shortly after hatching. Circumstantial evidence indicated that the blackflies *Simulium aureum* and *Cnephia minus* were the vectors of this parasite species. These blackflies occurred as adults and immatures during the time of *Leucocytozoon* transmission and engorged adults were collected after feeding on captive blue grouse. Dissections of engorged blackflies revealed that a small proportion of *S. aureum* possessed sporozoites and oocysts and that several *C. minus* possessed oocysts. No other hematophagous Diptera collected from grouse harbored sporozoites. Experimental transmission of sporozoites to uninfected blue grouse was not attempted.

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INTRODUCTION

Blood protozoa were first discovered from avian hosts by Danilewsky in 1885 from the Ukraine, shortly after malaria parasites were described from the blood of man. Ensuing workers reported the occurrence of these organisms in the blood of many birds and subsequently classified the majority of these parasites into the classes Sporozoa (Haemoproteidae, Leucocytozoidae, and Plasmodiidae) and Mastigophora (Trypanosomatidae). Filarioid nematode larvae (sub-family Splendidofilariinae) were also found to inhabit the vascular system during a portion of their life cycle. Members of the grouse family Tetraonidae were not examined for hematozoa until the early 1900's, when the British Grouse Commission attracted considerable attention to unusual mortalities of red grouse.

LEUCOCYTOZOON: Seligman and Sambon (1907) provisionally described *L. lovati* from the red grouse *(Lagopus scoticus)*, based on gametocyte morphology. Sambon (1908) described *L. mansoni* from the capercaillie *(Tetrao urogallus)* and Borg (1953) found this hematozoon in 59 percent of 599 capercaillie, black grouse *(Lyrurus tetrix)*, and hazel grouse *(Tetrastes bonasia)* in Sweden. Oliger (1940) claimed that *L. mansoni* was responsible for hazel grouse population fluctuations in the Gorkij region of Russia. In Ontario, Clarke (1934) attributed ruffed grouse *(Bonasa umbellus)* mortality to a leucocytozoid which he later (1935) described as *L. bonasae*. In 1938, Clarke reported his findings on the schizogony of *L. bonasae* in ruffed and spruce grouse *(Canachites canadensis)*. Bennett and Fallis (1960) found 60 percent of 75 ruffed grouse and 80 percent of 12 spruce grouse in Algonquin Park, Ontario, infected with *L. bonasae*.

Transmission studies of grouse leucocytozoa are notably scarce. Fallis and Davies (1949) reported that *L. bonasae* developed in the blackfly *Simulium venustum*. Fallis and Bennett (1958) successfully infected uninfected ruffed grouse chicks by inoculating a saline suspension of sporozoites from the blackflies *S. latipes* and *S. aureum* that had previously fed on infected grouse. They found these two simuliid species were responsible for transmission of *L. bonasae* in Algonquin Park. The sporogony of this parasite in blackflies was subsequently reported by Fallis and Bennett (1962) and was compared to that of *L. fringillinarum* Woodcock 1910 and *L. mirandae* Franca 1912. They found that sporogony was completed in some flies in less than 5 days at 22 C; others required 9, or more, days. *L. bonasae* oocysts (13.0 μ in diameter) were found to be intermediate in size between those of *L. fringillinarum* (10.9 μ) and *L. mirandae* (14.4 μ). No sporozoite measurements were given, although *L. bonasae* sporozoites were reported to be intermediate in size between those of *L. fringillinarum* (shorter and thicker) and *L. mirandae* (longer and more slender). Bennett (personal communication) states that there is much doubt about the validity of *L. bonasae*. Morphometric differences are not statistically different between gametocytes of *L. bonasae* and *L. lovati*, and Clarke (1935) himself stated that "the two species are closely related and any differences may be those of the host only."

HAEMOPROTEUS: Sambon (1908) recorded *H. mansoni* from red grouse, giving no description, and Fantham (1910) also found this haemoproteid in the same host, speculating that the grouse fly *(Ornithomya lagopodus)* was responsible for its transmission. Borg (1953) found that 16 percent of 599 capercaillie and black grouse examined were infected with *Haemoproteus*

(no species given) while hazel grouse were not. Clarke (1938), in Ontario, observed *Haemoproteus* in ruffed grouse, and gave an incomplete description of gametogony and schizogony. Fallis and Bennett (1960) described *H. canachites* from an adult spruce grouse and followed its sporogonic cycle in *Culicoides sphagnumensis*. They suggested that ornithophilic ceratopogonids were the probable vectors since they were known to feed on grouse, were very prevalent during *Haemoproteus* transmission, and since few (2) hippoboscids were collected from more than 300 grouse in various years. They found that mature microgametocytes exflagellated within three minutes after ingestion by *Culicoides*, and that zygotes (5.5 μ in diameter) were present in the stomach up to 12 hours later. Fifteen oocysts (averaging 6.3 μ) were found in the stomach wall four days after ingestion, and one day later developing sporozoites were seen within. Thirty oocysts averaged 9.5 μ and produced 20 to 30 sporozoites each averaging 11 to 14 μ. *Haemoproteus* oocysts resembled those of *Leucocytozoon*, differing only in their smaller size and by having pigment granules in the residual body. Sporozoites were structurally uniform in diameter and possessed rounded or slightly pointed ends. Prepatency was 14 days. Schizogony was not investigated by these authors.

Bennett *et al.* (1965) separated the genus *Haemoproteus* into *Haemoproteus* (hippoboscid vectors; prepatency greater than 14 days; large oocysts containing several hundred sporozoites) and *Parahaemoproteus (Culicoides* vectors; prepatency of 14 days; small oocysts containing fewer than 100 sporozoites). *Haemoproteus canachites* was placed in the latter category. These authors noted that separation of the proposed genera is difficult on gametocyte morphology alone and pointed out that hippoboscids were implicated as vectors for at least three species. Many other *Haemoproteus*

species occur in birds which do not normally harbor louse flies, and these haemoproteids would probably be shown to be transmitted by *Culicoides*. Levine and Campbell (1971) thought it premature to separate the genus as proposed; instead, they consider "the two genera" as sub-genera.

TRYPANOSOMA: Trypanosoma avium Danilewsky (1885) was first described from European owls (species not given) and roller-birds *(Coracias garrulus)*, using the names "majus" and "minus" for the large and small forms. In 1889, Danilewsky gave an account of *T. sanguinus avium* from a number of birds; however he did not designate a type host or provide an adequate description. Novy and McNeal (1905), Coatney and West (1938), Coatney and Roudabush (1937), and Bennett (1970a) used the terminology *T. avium* for trypanosomes in birds in North America. Baker (1956c) presented the best description of an avian trypanosome which he termed *T. avium*. Subsequent to Danilewsky's work, many authors have followed the "one host-one parasite" principle, describing species of avian trypanosomes based primarily on the avian host from which they were obtained. Bennett (1961) indicated that trypanosomes in most birds belong to the "avium" complex; within the complex many physiologically distinct strains or species may exist.

Avian trypanosomes are pleomorphic (ranging in size from 35 to 60 μ in length), contain a prominent kinetoplast posteriorly, and have a well developed undulating membrane and flagellum. *T. avium* occurs as trypomastigotes in the blood and bone marrow of avian hosts (Baker, 1956a) and as epimastigotes in the midgut and metacyclic trypanosomes in the hindgut of hippoboscids (Baker, 1956b) and simuliids (Bennett, 1961).

Anterior station infection takes place when birds ingest louse-flies, proceeds when the flagellates penetrate the buccal, esophagal, and/or crop membrane, and probably invade the lymphatic system (Baker, 1956b). Posterior station infection occurs when flagellates (in feces of the infected blackfly) penetrate breaks in the skin of birds, and development proceeds directly in the blood system (Bennett, 1961). The level of parasitemia is thought to be associated with the size of the inoculum since there has been no reported multiplication within the vertebrate, the trypanosomes simply become larger (Bennett, 1970a). After ingestion by the fly, trypomastigotes undergo three binary fissions, once in the midgut and twice in the hindgut, which produce many small epimastigotes. Optimal temperature for this process occurs at 15 to 20 C (Bennett, 1970b). In another study, Bennett (1970a) concluded that the apparent lack of pathogenicity, and vertebrate-host specificity (Bennett, 1961) indicates a long-standing avian host-parasite relationship.

MICROFILARIAE: Microfilariae are often encountered in surveys of avian blood parasites and are rarely, if ever, identified. Gibson (1965) intensively investigated the filarioid nematodes of all Tetraonidae from British Columbia and found hyperenzootic infections of *Microfilaria* sp. B. and *Skrjabinocta flexivaginalis* (Jones, 1961) in blue grouse from Nanaimo Lakes, Vancouver Island. *Microfilaria* sp. B. was prevalent in 89 percent of 56 adult male blue grouse, 72 percent of 29 adult females, and 62 percent of 16 yearlings; *Sk. flexivaginalis* was prevalent in 46 (82 percent), 20 (69 percent), and 6 (38 percent), respectively. In ruffed grouse of the same area, *Mf.* sp. B. was enzootic and *Sk. flexivaginalis* was sporadic. *Culicoides unicolor* group transmitted *Sk. flexivaginalis* from late June

to mid-August; *Mf.* sp. B. was vectored by *Cnephia minus* from early June to late July and by *Simulium aureum* from early June to early July and in early August. The latter blackfly species was a more efficient, but less abundant, intermediate host than the former. The prepatent period for both microfilariae was about 2 months. Infections with either microfilariae were found to be protracted or readily reacquired.

Coatney (1936, 1937) compiled a host-index and checklist of the species of *Haemoproteus* and *Leucocytozoon*, respectively. Herman (1944) listed the species occurring in North American birds. None of the above presented any data for the avian family Tetraonidae. Levine and Campbell (1971) and Hsu *et al.* (1973) have since compiled checklists of the valid species of *Haemoproteus* and *Leucocytozoon*, respectively, including those described from tetraonids. Braun and Willers (1967) have tabulated a checklist which includes the blood parasites of grouse in North America.

The presence of avian blood protozoa and filarioid nematode microfilariae in blue grouse *(Dendragapus obscurus* (Say)*)* has been documented by several researchers (Table I). Relatively few investigators (Fowle, 1946; Bendell, 1955) have supplemented prevalence findings with the degree of parasitemias (intensity) in these tetraonid hosts. Few (Woo, 1964; Gibson, 1965) have attempted, beyond speculation, to determine when, and by what means, these birds acquire their infections and to pursue these infections throughout the transmission season.

Fowle (1946) reported the occurrence of *Leucocytozoon*, *Haemoproteus* , and *Trypanosoma* and a microfilarioid nematode from two areas on Vancouver Island and found 56 percent of 44 grouse examined to be infected. In 1953, Adams and Bendell reported that *Leucocytozoon* occurred in 87 percent, *Haemoproteus* in 92 percent, *Trypanosoma* in 76 percent, and microfilariae

Table I. Prevalence of avian hematozoa in Blue Grouse in North America.

Author	No. Examined	No. Positive	*L*† No. Positive (%)	*H* No. Positive (%)	*T* No. Positive (%)	Mf No. Positive (%)	*P* No. Positive (%)	Locality
Fowle (1946)	44	26	8 (18)*	23 (52)	2 (5)*	5 (12)	††	Campbell River V.I., B.C.
Schottelius (1951)	16	8	3 (19)*	7 (44)	3 (19)	4 (25)	††	Methow Valley WA
Adams and Bendell (1953)	252	232	220 (87)*	232 (92)*	192 (76)*	217 (82)*	††	Quinsam Lake V.I., B.C.
Bendell (1955)	263	228	182 (69)*	228 (87)*	152 (58)*	139 (53)*	††	Quinsam Lake V.I., B.C.
Woo (1964)	62	62	62 (100)*	60 (97)*	54 (84)*	††	††	Nanaimo Lakes V.I., B.C.
Holmes and Boag (1965)	71	65	63 (89)	5 (7)*	9 (13)*	11 (15)	††	Gorge Creek ALTA
Stabler *et al.* (1969)	274	241	231 (84)	137 (50)	146 (53)	93 (34)	1 (0.4)	MT
King (1971)	50	40	40 (80)	28 (56)	36 (72)*	40 (80)*	3 (6)	Mt. Washington V.I., B.C.

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Table I. Prevalence of avian hematozoa in Blue Grouse in North America. - continued

Author	No. Examined	No. Positive	*L*† No. Positive (%)	*H* No. Positive (%)	*T* No. Positive (%)	Mf No. Positive (%)	*P* No. Positive (%)	Locality
Stabler *et al.* (1974)	55	53	48 (87)	19 (35)*	25 (46)	28 (51)*	2 (4)	CO
This Study (1975)	688	541	541 (79)	395 (57)	311 (45)	186 (27)	††	Comox Burn V.I., B.C.

† *L* = *Leucocytozoon*, *H* = *Haemoproteus*, *T* = *Trypanosoma*, Mf = Microfilaria, *P* = *Plasmodium*

†† Not reported.

* Statistically different ($P < 0.01$) from that in the present study.

in 82 percent of 252 birds at Quinsam Lake, near Campbell River, Vancouver Island. Bendell (1955) indicated that 174 yearlings and adults from the same area harbored *Leucocytozoon* (85 percent), *Haemoproteus* (97 percent), *Trypanosoma* (77 percent) and microfilariae (80 percent) during the spring and summer of 1950 to 1952. He also examined 89 chicks (no ages given) which possessed a lower prevalence (*Leucocytozoon* 38 percent, *Haemoproteus* 66 percent, *Trypanosoma* 18 percent, and microfilariae 0 percent). Woo (1964) examined 62 grouse near Nanaimo Lakes, Vancouver Island which harbored *Leucocytozoon* (100 percent), *Haemoproteus* (97 percent), and *Trypanosoma* (84 percent). He proposed that a new species, *Haemoproteus dendragapi*, be erected on the basis of round gametocytes found concurrently with those of *Haemoproteus canachites* Fallis and Bennett 1960. He thought that his *Leucocytozoon "A"* was also probably a new species. Gibson (1965) investigated the taxonomy and transmission of microfilarioid nematodes in tetraonids in British Columbia and found only *Microfilaria* sp. B. and *Skrjabinocta flexivaginalis* infecting blue grouse on Vancouver Island. The former was found to be transmitted by *Cnephia minus* and *Simulium aureum*; the latter, by *Culicoides unicolor* group. King (1971), in a subalpine study, found 80 percent of 50 blue grouse to be infected with one or more of the above blood parasites during 1965 and 1966. He concluded that infection rates were similar to those found in the lowlands (Bendell, 1955), except for a lower prevalence of *Haemoproteus* (56 percent).

ORNITHOPHILIC BLACKFLIES: Sommerman *et al.* (1955) reported one to two generations of *Simulium aureum* annually in Alaska and Davies (1950) reported form "A" was bivoltine in Ontario. Abdelnur (1968), and Anderson and Dicke (1960), reported three generations annually in Alberta, and

Wisconsin. Peterson (1956) and Wolfe and Peterson (1959) reported that eggs are the over-wintering stage and Sommerman *et al.* (1955) found that the first generation hatched in mid-May and the second began in early July in Alaska. They also found that larvae require 2 to 4 weeks for development and one week for pupae. Newly emerged females have undeveloped eggs and little stored nutrients (Abdelnur, 1968) and oviposit in patchily vegetated streams (Davies and Peterson, 1956). Anderson and DeFoliart (1961), Fallis and Bennett (1958, 1962), Jamnback (1969) and Stone (1964) reported *S. aureum* to be ornithophilic, and a vector of *Leucocytozoon* and *Trypanosoma* of birds. Hearle (1932) reported that larvae, pupae and adults of *Cnephia minus* occurred in the Cariboo District, British Columbia, but that nothing was known of its blood-sucking habit. Sommerman *et al.* (1955) reported that one generation occurred in Alaska during late spring, but never collected immatures. Sommerman *et al.* (1955) collected adults in Alaska until mid-June. Little is known about the biology of this species. Woo (1964) and Gibson (1965) found adult *C. minus* engorged on grouse and harboring sporozoites and microfilariae on Vancouver Island.

Shewell (1955) suggested that the large basal tooth on the tarsal claw of several species of blackflies is an adaptation for feeding on birds. Of 22 North American species possessing bifid claws, 9 species are known to feed preferentially on birds (Fallis, 1964). There are strong indications that *Cnephia minus* is composed of two closely allied forms. Dunbar (1959) reported that *Simulium aureum* consists of 7 cytological forms, five of which are North American in distribution. It should be strongly emphasized that the taxonomic status of all hematophagous Diptera from Vancouver Island, and for that matter, western Canada, is poorly known.

OBJECTIVES OF THE STUDY: Prompted by the knowledge that hematozoa were frequently found in blue grouse, and by the paucity of relevant information on transmission, I set out to determine, first, the relative prevalence and intensity rates in this host, second, when blue grouse acquired blood parasite infections, and third, the cycle of transmission of *Leucocytozoon bonasae*. Initially attention was focused on the blood parasites of blue grouse alone, because 1) in many regions of Vancouver Island this is by far the most abundant native galliform, 2) research into its population dynamics was already well advanced and 3) accomodation for field research was available.

Since blue grouse *Dendragapus obscurus fuliginosus* (Ridgway) are resident in most montane regions of Vancouver Island their distribution often overlaps that of ruffed grouse and non-tetraonid birds, species for which knowledge of hematozoon infections are entirely lacking. Therefore, when considerable data had been acquired on the hematozoa of blue grouse, the study was expanded to include infections in other birds. Additionally, information on blackfly population composition, distribution, and abundance was monitored to further knowledge of that vector's biology and possible interactions with the host.

MATERIALS AND METHODS

CAPTURE OF BIRDS: Blue grouse were found with the aid of English pointing dogs, captured with extendible noosing poles (Zwickel and Bendell, 1967), banded, measured for physical parameters, bled, and released unharmed. Birds were sampled from April until September, 1973 and 1974. Recapture was not possible since each bird was a valuable portion of an on-going population dynamics study in which birds were not recaptured.

Non-tetraonid birds were captured during the period May 20 to August 27, 1974, in 3.1 cm mesh, 2.1 x 9.5 m Japanese mist nets. Nets were placed in areas of adequate cover and high bird densities to maximize the number caught. These birds were marked by toe-nail clipping combinations, bled, and then released. Identification of difficult species was verified by an ornithologist, M. K. McNicholl, a participant in the grouse population study. Between netting sessions, mist nets were left strung in the field, gathered at the center to form a tight cord, and bound with elastic bands in order to facilitate rapid unfurling for the next capture period. We observed that birds tended to fly under, over, or perched on the gathered nets and, later, often responded by "flaring" into the nets when they were unfurled. Capture periods extended from early morning (0500 hours PDST) until noon and from early evening (1700 hours PDST) until dusk (2100 hours PDST) on those days when conditions were optimal for catch. Usually four capture periods per week of 10 man-hours per day were made.

BLOOD SMEARS: Blood was obtained from grouse and larger passerine species by venipuncture of the brachial or cubital vein, and from smaller species from blood eminating from toe-nail clips. A small drop of blood was transferred to the slide and a thin blood smear was quickly made before clotting occurred. Each blood slide from blue grouse was identified by the bird band number. Slides from non-tetraonid birds were sequentially numbered. Blood smears were fixed in absolute methanol for two minutes the same day they were made and were stained in Giemsa's solution for one hour, buffered at pH 7.2 for maximal differentiation.

Examination of blood smears was made, initially, at low magnifications of 100x and 400x to ascertain the presence of parasites, and subsequently, at 1000x magnification for confirmation of identification. Quantification of parasites was recorded as the number seen per 10,000 erythrocytes.

STATISTICAL ANALYSES: Prevalences of blood parasites in adult, yearling and juvenile blue grouse for each year were analyzed for statistical differences. A binomial t-test, weighted for sample size by degrees of freedom (Sokal and Rohlf, 1969), was used to test for equality of prevalences at the $P < 0.01$ level. Mean intensities of parasite infections between different sexes and age classes were analyzed by Student's *t*-test for significant differences at the $P < 0.01$ level. The calculated critical value was adjusted for degrees of freedom of sample sizes (Sokal and Rohlf, 1969).

HOST-BAITING EXPERIMENTS: Three blue grouse were incubated from eggs during 1973, maintained over the winter in Edmonton, Alberta, and used as live attractants during 1974, since wild caught birds quickly succumb

to the stresses imposed by confinement. A captive grouse was placed in a 42 x 30 x 36 cm wire cage and was elevated by a system of ropes and pulleys (Bennett, personal communication) to varying heights (0 to 8.5 m) above ground during different times of day. A dark cloth hood placed over the bird's head kept the animal relatively quiet during exposure so that flies were able to feed without being dislodged. Grouse were chosen sequentially for exposure so as not to introduce individual bias.

The grouse was exposed for 20 minutes after which time the cage was gently lowered onto a 1 m^2 plywood square. An insect-proof cage (76 x 76 x 76 cm), covered with 200 mesh fiberglass fabric, was immediately placed over the exposure cage. Rubber welt strips glued to the bottom of the collecting cage formed a tight seal, preventing the escape of any flies. All flies which had left the bird and settled on the sides of the collecting cage were aspirated through 15 cm diameter muslin sleeves (on the two opposite sides of the collecting cage) and were placed into one half pint round ice-cream containers (Collins and Jefferey, 1950). Birds were exposed at Comox Burn during the period 15 May to 25 August, 1974. Records from previous years (Gibson, 1965; Woo, 1964) indicated that the height of the biting fly season occurred the last three weeks of June.

Engorged flies were maintained in ice-cream containers at ambient environmental temperature under reduced light conditions. Flies were fed a 5 percent sucrose-water solution *ad lib* and wet cotton plugs were placed on top of each container to provide high humidity.

FLY DISSECTIONS: Flies were maintained for a period of 72 hours for the sexual development of the parasite (extrinsic incubation period) to take place. The flies were then chilled for 1 to 2 minutes to reduce movements, the stomach and salivary glands were dissected in saline (Shute and Maryon, 1966), and ovarian development was initially examined for the physiologic status of the fly (Detinova, 1962). Stomachs and salivary glands were expressed onto glass slides, quickly air-dried, and then fixed in absolute methanol for one minute. Stomachs were stained with a 2 percent solution of mercurochrome (Eyles, 1950) as this method stained oocysts deeply red without marked staining of fly tissue. Salivary glands were stained in Giemsa's solution for one hour. Parasitic stages were examined by compound microscopy at 400x and 1000x magnifications.

VECTOR SAMPLING: Immature blackflies were collected weekly from June 10 to August 28, 1974 from 10 x 10 cm ceramic tiles (Lewis and Bennett, 1974) randomly placed in a complex of streams throughout the study area. Larvae and pupae were placed into vials containing 70 percent ethanol, and water temperature and depth measurements were recorded for each site. Species determinations were made and verifications were kindly provided by Dr. B. V. Peterson, Head of Diptera Section, Agriculture Canada, Ottawa.

Adult blackfly censusing attempts were carried out with standardized sweep net collections (40 sweeps per minute), taken at random intervals, with and without grouse as attractants. Representative specimens were sorted to genera, their heads and genitalia were dissected and mounted, and they were identified by Dr. Peterson.

Other hematophagous Diptera caught were initially identified to family level, pinned or preserved in 70 percent ethanol, and representative specimens were sent to specialists for identifications. Dr. Willis W. Wirth, Research Entomologist, USDA Systematic Entomology Laboratory, Washington, D.C., kindly identified ceratopogonids. Dr. Stephen Smith, University of Waterloo, is currently examining specimens of Culicidae caught in sweep net collections. No Tabanidae were collected from grouse.

STUDY AREA: The present study was carried out on an approximate 1500 hectare area (49° 45', 125° 10') on the east slope of Vancouver Island, 16 km west of Courtenay, British Columbia. Comox Burn, as denoted in this study, includes two large areas being used in a population ecology study of blue grouse: Comox Burn (485 hectares), Tsolum Main (625 hectares), and 2 km buffer zone between the two. The area is in a region intermediate between the douglas fir *(Pseudotsuga menziesii)* and western hemlock *(Tsuga heterophylla)* bioclimatic zones (Krajina, 1959). This area was clearcut between 1947 and 1969, ravaged by a wild fire in September 1961, and has since been replanted as a douglas fir plantation. The area ranges in elevation from 244 m to 670 m above sea level. A more complete description of the area has been previously reported (Zwickel, 1972).

RESULTS

HEMATOZOA FROM BLUE GROUSE

A total of 688 adult, yearling, and juvenile blue grouse *(Dendragapus obscurus fuliginosus* (Ridgway)*)* from Comox Burn, Vancouver Island, were examined for blood parasites during the spring and summer of 1973 and 1974. Eighty-four percent (577) of those grouse harbored infections of one or more of the following hematozoa: *Leucocytozoon bonasae* Clarke 1935, *Haemoproteus (Parahaemoproteus) canachites* Fallis and Bennett 1960, *Trypanosoma avium* Danilewsky 1885, and microfilariae (probably *Microfilaria* sp. B. of Gibson, 1965).

In 1973, 351 of 381 (92 percent) grouse were infected, with concurrent infections occurring in 91 percent of those infected. In 1974, however, only 74 percent (226) of 307 grouse examined harbored infections; 54 percent had concurrent infections. Table II summarizes the prevalence and intensity data for each species of parasite and also provides information for those birds which were concurrently infected.

LEUCOCYTOZOON: Prevalence and intensity data for different age classes and sexes of blue grouse, for each year and both years, are presented in Table III. No statistical difference was found between intensities of infection in yearlings and adults within years; however, prevalences and intensities of all groups between years were significantly different.

Figure I depicts seasonal prevalence data for infections of *L. bonasae* in all age classes of blue grouse for 1973 and 1974. Each month of the sample period was divided into 4 equal periods: 1 to 4 . Figure II illustrates the mean intensities of infection of *L. bonasae* in blue

Table II. Prevalence and intensity of avian hematozoa in Blue Grouse from Comox Burn, Vancouver Island.

		Parasite Species				Infections		
		L†	*H*	*T*	Mf	Double	Triple	Quadruple
1973 N = 381	No. Infected	328	297	256	162	70	128	122
	Prevalence (%)	86*	78*	67*	43*	18*	37*	32*
	Intensity†† (mean ± S.E.)	27.1* (±2.25)	21.1* (±1.55)	2.8* (±0.14)	2.8* (±0.22)	6.7* (±1.21)	16.3* (±2.17)	18.8* (±1.89)
1974 N = 307	No. Infected	213	98	55	24	85	35	3
	Prevalence (%)	69*	32*	18*	8*	28*	11*	1*
	Intensity (mean ± S.E.)	5.7* (±0.44)	92.9* (±7.38)	1.2* (±0.07)	1.4* (±0.23)	18.6* (±2.71)	10.4* (±2.30)	1.4* (±0.86)
Total N = 688	No. Infected	541	395	311	186	155	163	125
	Prevalence (%)	79	57	45	27	23	24	18
	Intensity (mean ± S.E.)	18.7 (±1.44)	38.9 (±2.67)	2.5 (±0.12)	2.6 (±0.20)	12.1 (±1.40)	13.7 (±1.58)	11.0 (±1.16)

† *L* = *Leucocytozoon*, *H* = *Haemoproteus canachites*, *T* = *Trypanosoma avium*, Mf = Microfilaria

†† Mean number of parasites per 10,000 erythrocytes.

* $P < 0.01$.

Table III. Prevalence and intensity of *Leucocytozoon bonasae* in different age classes and sexes of Blue Grouse from Comox Burn, Vancouver Island.

		Adults			Yearlings			Juveniles	Grand
		Male	Female	Total	Male	Female	Total	Total	Total
1973	No. Examined	64	53	117	49	70	119	145	381
	No. Infected	64	52	116	47	68	115	97	328
	Prevalence (%)	100	98*	99*	96	97	97	67*	86*
	Intensity† (mean ± S.E.)	20.7* (±3.12)	22.6* (±2.89)	21.6* (±2.15)	18.8* (±2.34)	38.1* (±5.16)	28.4* (±3.27)	32.1* (±5.99)	27.1* (±40.7)
1974	No. Examined	25	58	83	19	59	78	146	307
	No. Infected	23	52	75	16	53	69	69	213
	Prevalence (%)	92	90*	90*	84	90	8.8	47*	69*
	Intensity (mean ± S.E.)	4.7* (±0.70)	5.3* (±1.44)	5.1* (±1.02)	6.4* (±1.02)	6.2* (±0.47)	6.2* (±0.43)	6.0* (±0.69)	5.7* (±0.44)

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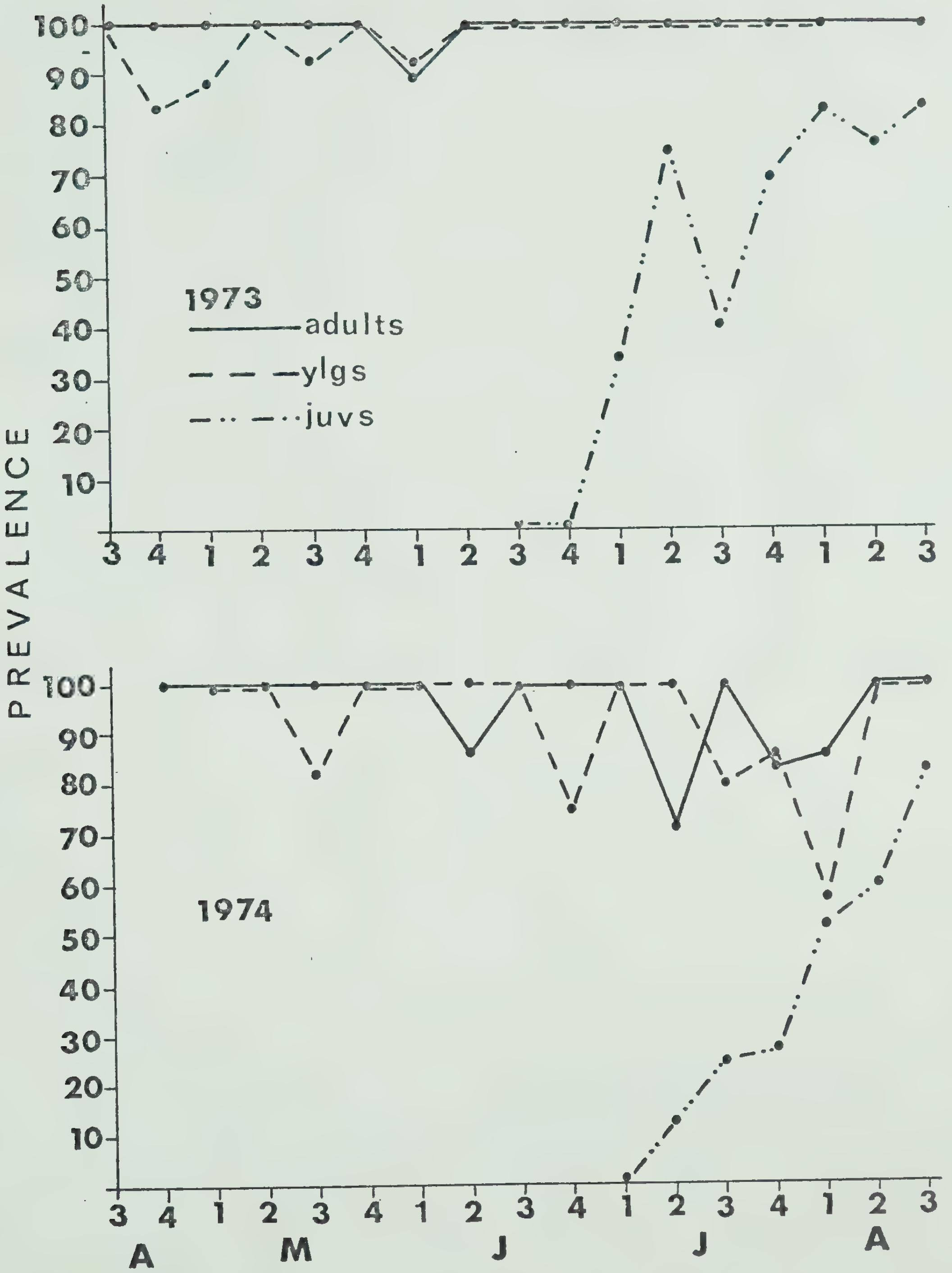
Table III. Prevalence and intensity of *Leucocytozoon bonasae* in different age classes and sexes of Blue Grouse from Comox Burn, Vancouver Island. - continued

		Adults			Yearlings			Juveniles	Grand
		Male	Female	Total	Male	Female	Total	Total	Total
Total Years	No. Examined	89	111	200	68	128	197	291	688
	No. Infected	87	104	191	63	121	184	166	541
	Prevalence (%)	98	94	96	93	92	93	57	79
	Intensity (mean ± S.E.)	16.5 (±2.4)	14.0 (±1.82)	15.1 (±1.48)	15.7 (±1.84)	22.4 (±3.18)	20.1 (±2.20)	21.3 (±3.65)	18.7 (±1.44)

† Mean number of parasites per 10,000 erythrocytes.

* $P < 0.01$.

Figure I. Seasonal prevalence of *Leucocytozoon bonasae* in different age classes of Blue Grouse from Comox Burn, Vancouver Island, 1973 and 1974.


PREVALENCE
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adults
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1974
3 4 1 2 3 4 1 2 3 4 1 2 3 4 1 2 3
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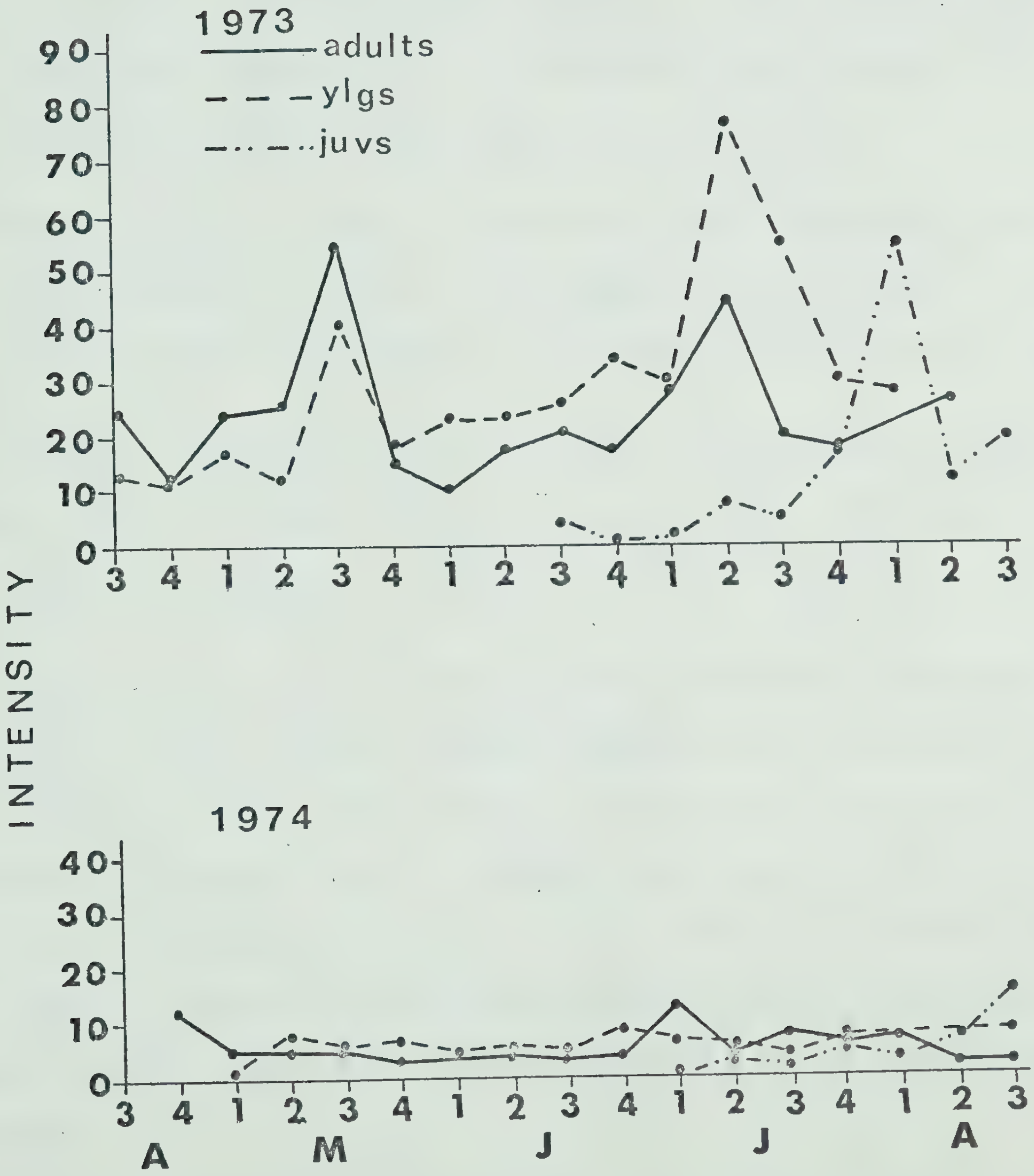
FIGURE II. Seasonal intensity of *Leucocytozoon bonasae* in different age classes of Blue Grouse from Comox Burn, Vancouver Island, 1973 and 1974.


1973
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INTENSITY
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3 4 1 2 3 4 1 2 3 4 1 2 3 4 1 2 3
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grouse for each year. Figure III shows the total intensity of all age classes for each year.

HAEMOPROTEUS: The prevalence and intensity of *H. canachites* in blue grouse is presented in Table IV. Mean intensities of infection in male and female adults were significantly different, as were those in male and female yearlings. Figures IV to VI summarize weekly prevalence and intensity data for each age class and sex for both years.

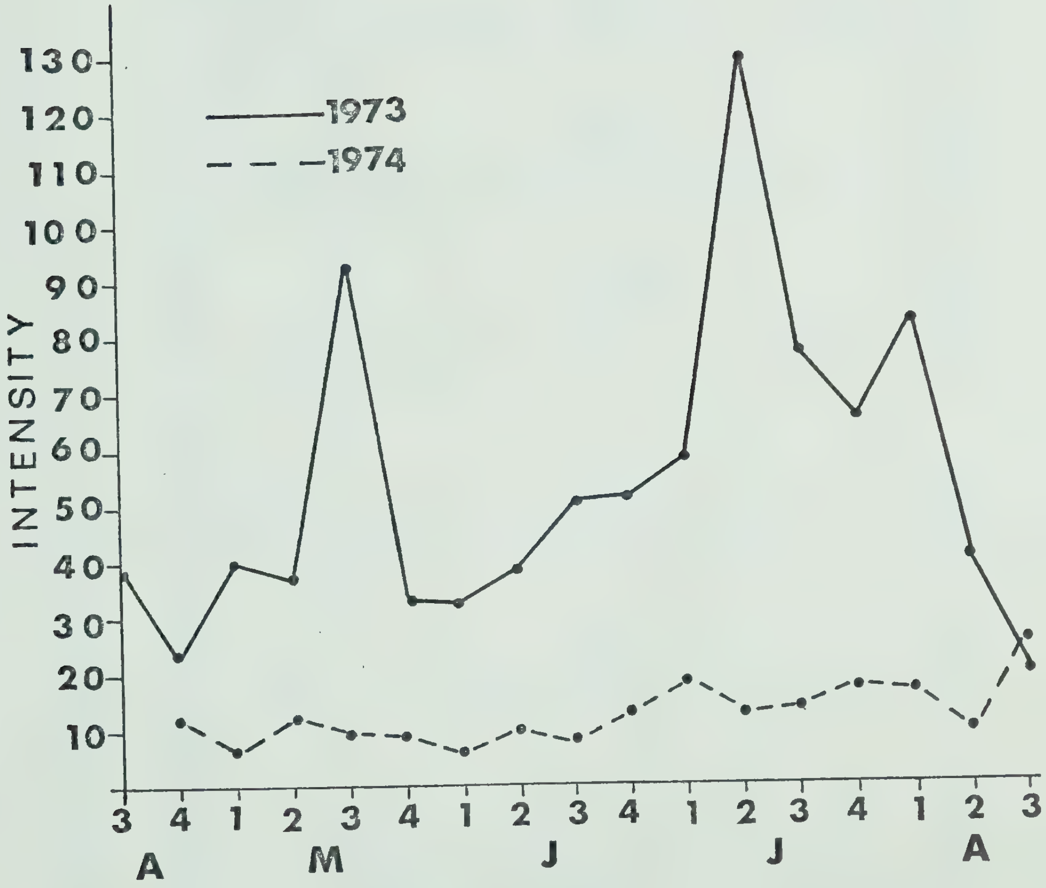
TRYPANOSOMA: Table V presents *T. avium* prevalence and intensity data for all age classes for 1973 and 1974. Figures VII and VIII present weekly prevalence and intensity of infections for each age class for both years.

MICROFILARIAE: Prevalence and intensity data for microfilarial infections in blue grouse in 1973 and 1974 are presented in Table VI. Figure IX shows the weekly prevalence of microfilariae for each age class each year.

Other hematozoa were not found in any of the grouse examined from Comox Burn. However, Bennett (personal communication) has personally shown me slides of blue grouse infected with at least three species of *Plasmodium: P. circumflexum, P. relictum,* and *P. vaughni,* from the Quinsam Lake area, 30 km north of Comox Burn. J. F. Bendell had, for some years, deposited 478 slides with the WHO International Reference Center for Avian Malaria Parasites and 13 percent were positive for one or more of these parasites.

APPEARANCE OF HEMATOZOA IN CAPTIVE CHICKS: Seventy-five captive blue grouse chicks were monitored for the appearance of avian hematozoa in 1973. Eggs were collected from Comox Burn and Quinsam Lake study areas and were incubated. Three days after hatching, chicks were placed in a chicken

Figure III. Total seasonal prevalences of *Leucocytozoon bonasae* in different age classes of Blue Grouse from Comox Burn, Vancouver Island, 1973 and 1974.


1973
1974
INTENSITY
130
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100
90
80
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Table IV. Prevalence and intensity of *Haemoproteus canachites* in different age classes and sexes of Blue Grouse from Comox Burn, Vancouver Island.

		Adults			Yearlings			Juveniles	Grand
		Male	Female	Total	Male	Female	Total	Total	Total
1973	No. Examined	64	53	117	49	70	119	145	381
	No. Infected	56	49	105	45	55	100	92	297
	Prevalence (%)	88	92	90	92*	79*	84*	63*	78
	Intensity† (mean ± S.E.)	20.2 (±3.11)	27.5* (±5.88)	23.6 (±3.21)	20.2* (±3.29)	23.2* (±2.40)	21.9* (±1.97)	17.4 (±2.66)	21.1* (±1.55)
1974	No. Examined	25	58	83	19	59	78	146	307
	No. Infected	16	48	64	4	26	30	4	98
	Prevalence (%)	64	83	77	21*	44*	38*	3*	32
	Intensity (mean ± S.E.)	60.1 (±16.1)	108.6* (±11.0)	96.5 (±9.48)	2.5* (±0.87)	102* (±12.4)	88.7* (±12.4)	65.8 (±37.8)	92.9* (±7.38)

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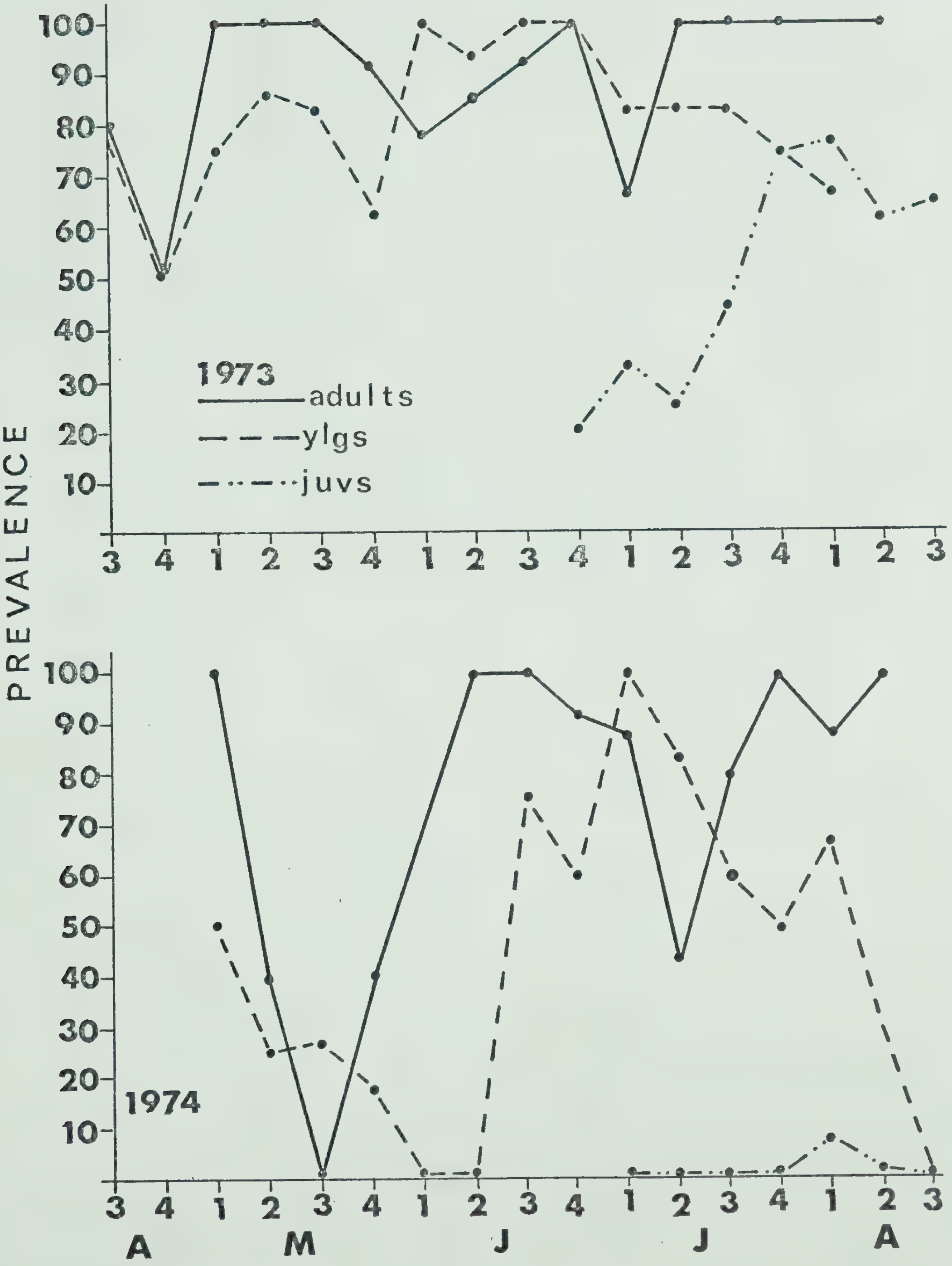
Table IV. Prevalence and intensity of *Haemoproteus canachites* in different age classes and sexes of Blue Grouse from Comox Burn, Vancouver Island. - continued

		Adults			Yearlings			Juveniles	Grand
		Male	Female	Total	Male	Female	Total	Total	Total
Total Years	No. Examined	89	111	200	68	128	197	291	688
	No. Infected	72	97	169	49	81	130	96	395
	Prevalence (%)	81	87	85	72	63	66	33	57
	Intensity (mean ± S.E.)	29.1 (±4.68)	67.7 (±7.42)	51.2 (±4.92)	18.7 (±3.1)	48.5 (±5.92)	37.3 (±4.06)	19.4 (±30.6)	38.9 (±2.67)

† Mean number of parasites per 10,000 erythrocytes.

* $P < 0.01$.

Figure IV. Seasonal prevalence of *Haemoproteus canachites* in different age classes of Blue Grouse from Comox Burn, Vancouver Island, 1973 and 1974.


PREVALENCE
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1974
3 4 1 2 3 4 1 2 3 4 1 2 3 4 1 2 3
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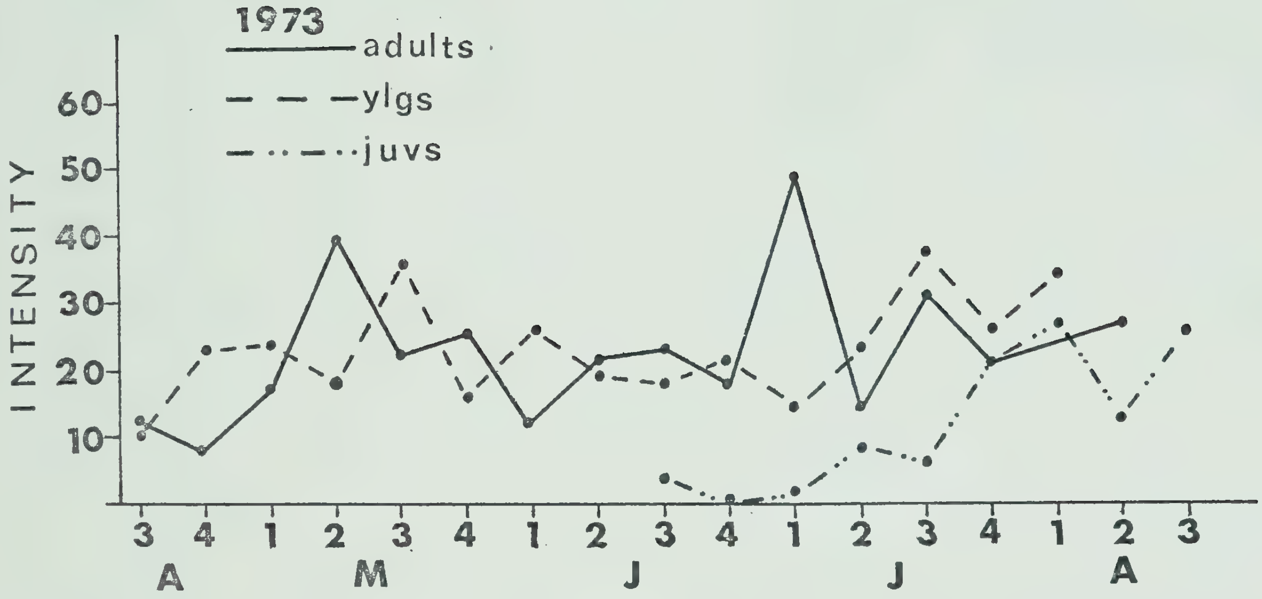
Figure V. Seasonal intensity of *Haemoproteus canachites* in different age classes of Blue Grouse from Comox Burn, Vancouver Island, 1973.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INTENSITY
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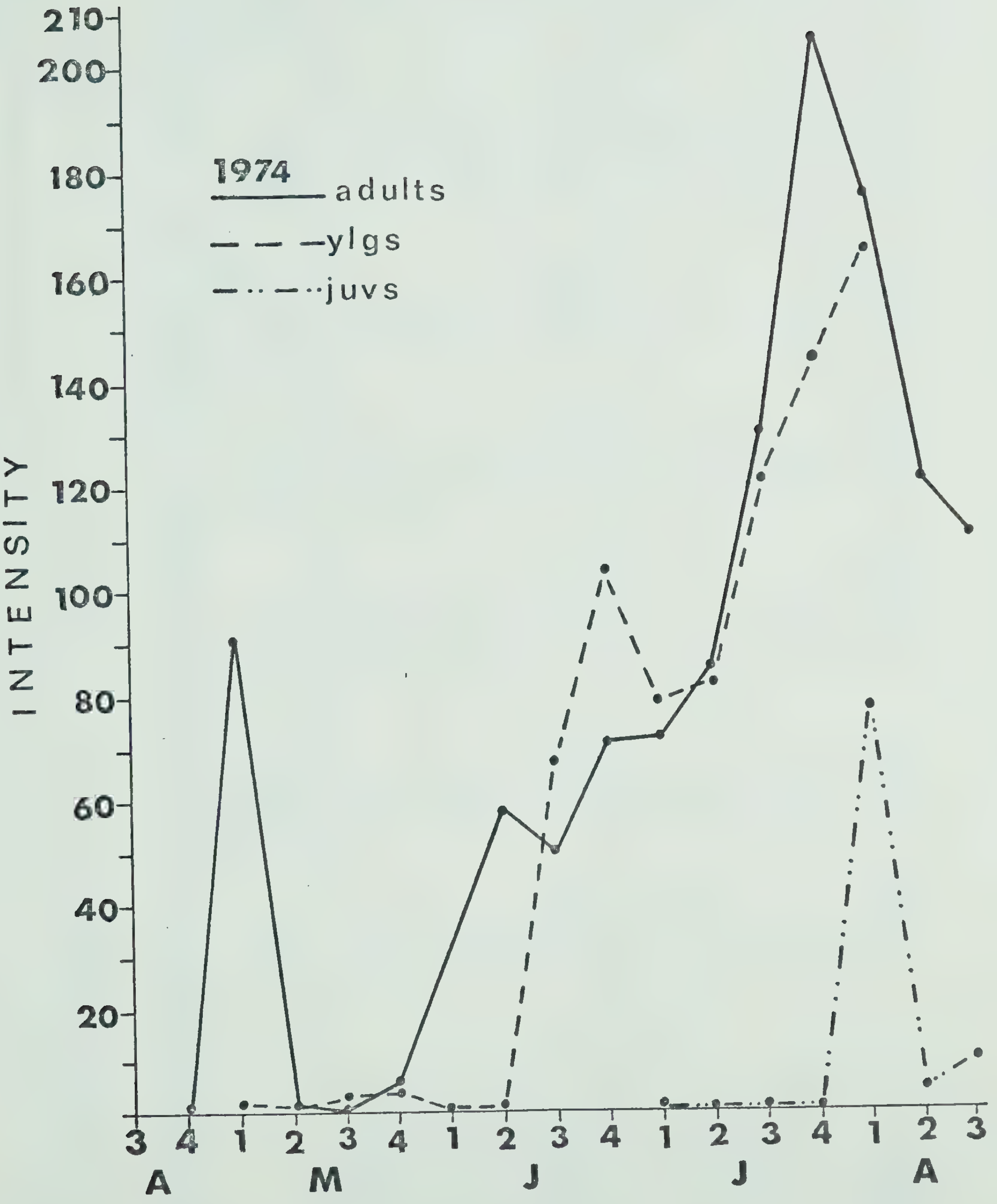
Figure VI. Seasonal intensity of *Haemoproteus canachites* in different age classes of Blue Grouse from Comox Burn, Vancouver Island, 1974.


1974
adults
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INTENSITY
210
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160
140
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Table V. Prevalence and intensity of *Trypanosoma avium* in different age classes and sexes of Blue Grouse from Comox Burn, Vancouver Island.

		Adults			Yearlings			Juveniles	Grand
		Male	Female	Total	Male	Female	Total	Total	Total
1973	No. Examined	64	53	117	49	70	119	145	381
	No. Infected	50	50	100	33	50	83	73	256
	Prevalence (%)	78*	94*	85*	67*	71*	70*	50*	67*
	Intensity† (mean ± S.E.)	2.9* (±0.31)	3.2* (±0.37)	3.0* (±0.24)	2.1 (±0.24)	2.6* (±0.28)	2.4* (±0.20)	3.0* (±0.28)	2.8* (±0.14)
1974	No. Examined	25	58	83	19	59	78	146	307
	No. Infected	10	15	25	6	14	20	10	55
	Prevalence (%)	40*	26*	30*	32*	24*	26*	7*	18*
	Intensity (mean ± S.E.)	1.4* (±0.22)	1.1* (±0.09)	1.2* (±0.10)	1.3 (±0.21)	1.2* (±0.15)	1.3* (±0.12)	1.2* (±0.2)	1.2* (±0.07)

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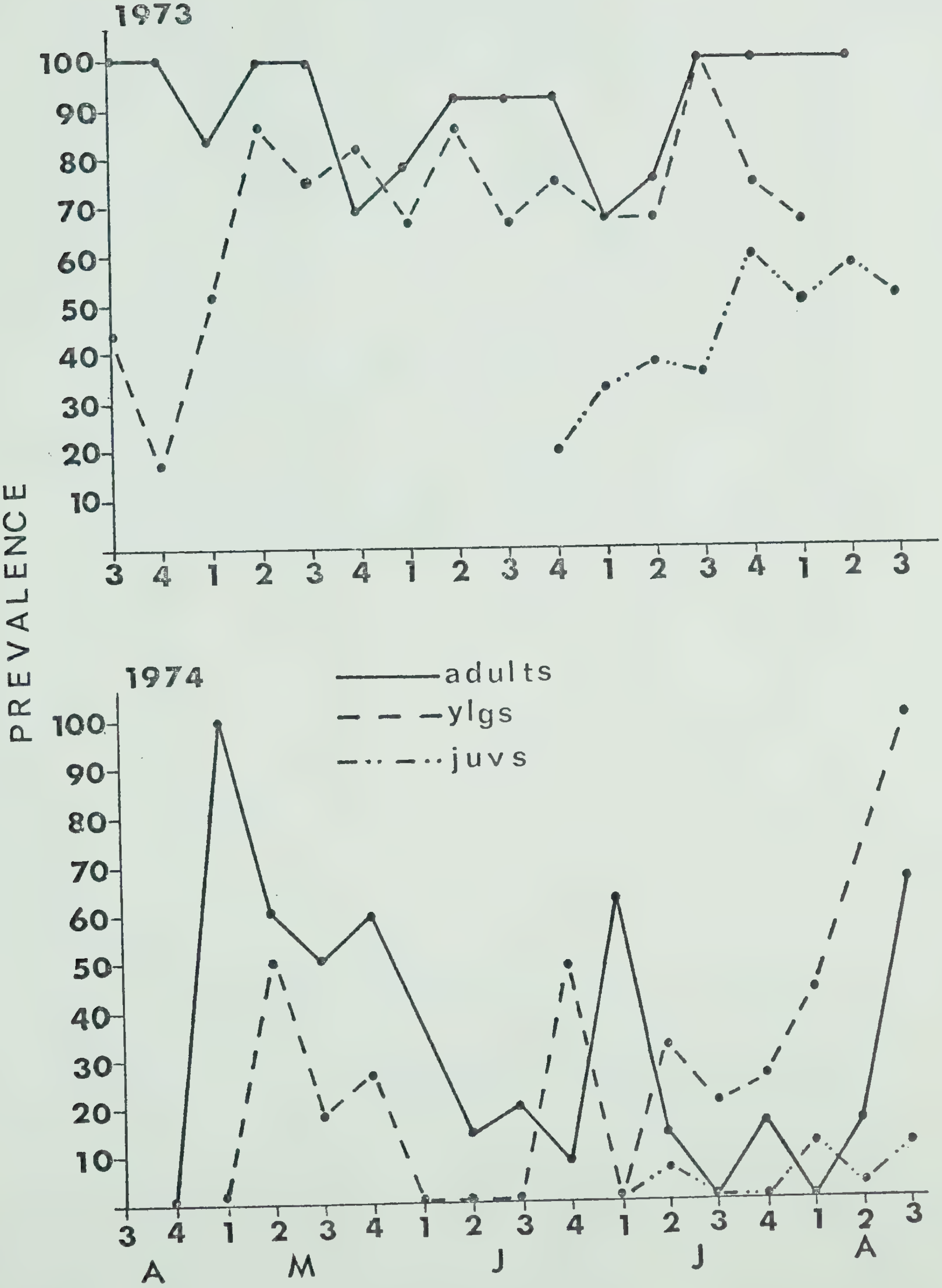
Table V. Prevalence and intensity of *Trypanosoma avium* in different age classes and sexes of Blue Grouse from Comox Burn, Vancouver Island. - continued

		Adults			Yearlings			Juveniles	Grand
		Male	Female	Total	Male	Female	Total	Total	Total
Total Years	No. Examined	89	111	200	68	128	197	291	688
	No. Infected	60	65	125	39	64	103	83	311
	Prevalence (%)	67	59	63	57	50	52	29	45
	Intensity (mean ± S.E.)	2.7 (±0.27)	2.7 (±0.30)	2.7 (±0.20)	2.0 (±0.21)	2.3 (±0.23)	2.2 (±0.17)	2.8 (±0.26)	2.5 (±0.12)

† Mean number of parasites per 10,000 erythrocytes.

* $P < 0.01$.

Figure VII. Seasonal prevalence of *Trypanosoma avium* in different age classes of Blue Grouse from Comox Burn, Vancouver Island, 1973 and 1974.


1973
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PREVALENCE
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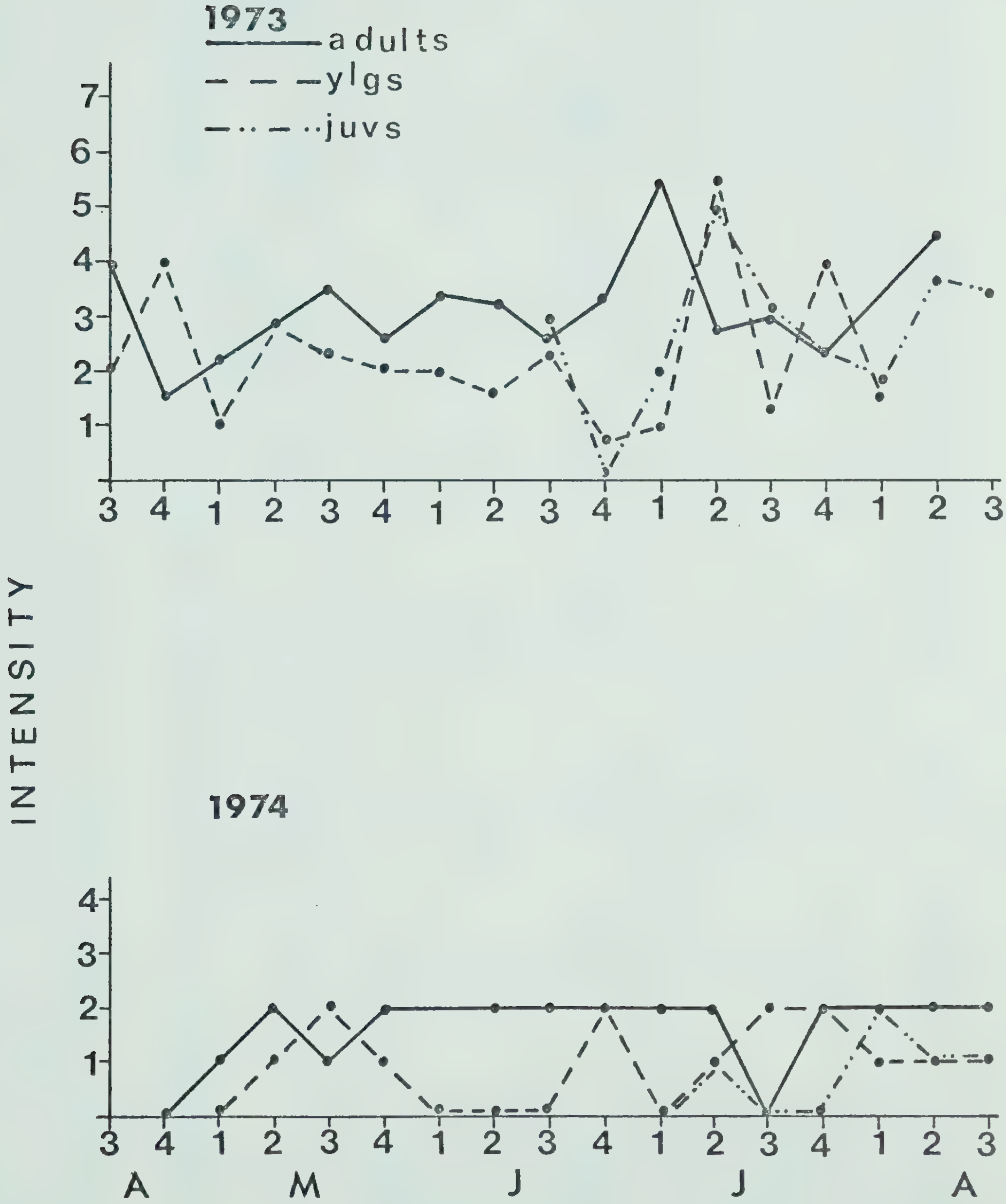
Figure VIII. Seasonal intensity of *Trypanosoma avium* in different age classes of Blue Grouse from Comox Burn, Vancouver Island, 1973 and 1974.


1973
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INTENSITY
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Table VI. Prevalence and intensity of microfilariae in different age classes and sexes of Blue Grouse from Comox Burn, Vancouver Island.

		Adults			Yearlings			Juveniles	Grand
		Male	Female	Total	Male	Female	Total	Total	Total
1973	No. Examined	64	53	117	49	70	119	145	381
	No. Infected	46	29	75	22	26	48	39	162
	Prevalence (%)	72*	55*	64*	45	37*	40*	27*	43*
	Intensity† (mean ± S.E.)	3.0* (±0.43)	3.4 (±0.81)	3.1 (±0.40)	2.2* (±0.41)	2.96* (±0.49)	2.6* (±0.33)	2.2 (±0.27)	2.8* (±0.22)
1974	No. Examined	25	58	83	19	59	78	146	307
	No. Infected	4	9	13	3	7	10	1	24
	Prevalence (%)	16*	16*	16*	16	12*	13*	0.7*	8*
	Intensity (mean ± S.E.)	1* (±0.0)	1.2 (±0.22)	1.2 (±0.15)	1* (±0.0)	2.1* (±0.70)	1.8* (±0.51)	1 (±1.0)	1.4* (±0.23)

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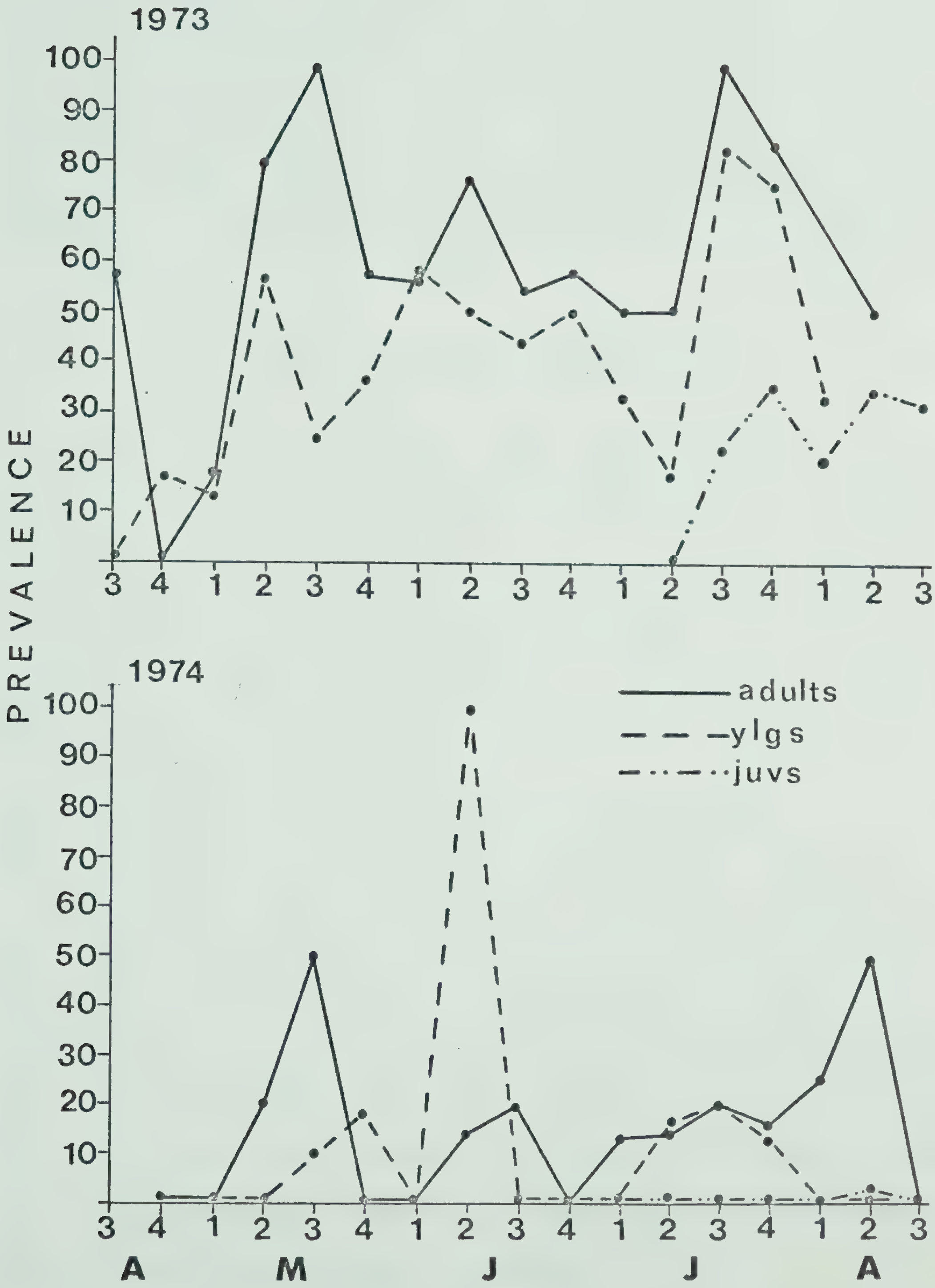
Table VI. Prevalence and intensity of microfilariae in different age classes and sexes of Blue Grouse from Comox Burn, Vancouver Island. - continued

		Adults			Yearlings			Juveniles	Grand
		Male	Female	Total	Male	Female	Total	Total	Total
Total Years	No. Examined	89	111	200	68	128	119	291	688
	No. Infected	50	38	88	25	33	58	40	186
	Prevalence (%)	56	34	44	37	26	49	14	27
	Intensity (mean ± S.E.)	2.8 (±0.40)	2.9 (±0.63)	2.9 (±0.35)	2.0 (±0.36)	2.8 (±0.41)	2.5 (±0.28)	2.2 (±0.27)	2.6 (±0.20)

† Mean number of parasites per 10,000 erythrocytes.

* $P < 0.01$.

Figure IX. Seasonal prevalence of microfilariae in different age classes of Blue Grouse from Comox Burn, Vancouver Island, 1973 and 1974.


1973
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PREVALENCE
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wire-enclosed outdoor aviary. It should be pointed out that the aviary was located within an area of dense alders, an area dissimilar to normal blue grouse habitat. Additionally, this aviary was located 36 km north of Comox Burn at the head of Gooseneck Lake. Blood smears were taken from each chick on three occasions: July 16 and 28 and August 3, 1973. Table VII presents the initial period of time after exposure when hematozoa were first detected. No concurrent infections were noted.

HEMATOZOA FROM NON-TETRAONID BIRDS

A total of 119 individuals, comprising 28 species of 8 passerine and 2 other non-tetraonid families from Comox Burn, were examined for the presence of hematozoa during the period 20 May to 27 August, 1974 (Appendix I). Thirty-four percent (68) of the birds were infected by one or more species of avian hematozoa (Table VIII). Only one bird, a dark-eyed junco, *Junco hyemalis*, was infected with microfilariae. Prevalence and intensity data of hematozoa are presented in Table VIII. Multiple infections were found in 14 percent of the infected birds: 7 birds had concurrent infections of *Leucocytozoon* and *Haemoproteus* and 3 birds had concurrent infections of *Leucocytozoon* and *Trypanosoma*. Twenty-one juvenile and 48 adult birds harbored infections. Monthly prevalence rates were highest in June (38 percent of 84 birds) and equal in July (33 percent of 72 birds) and August (32 percent of 40 birds). Only one infected bird was captured in May. A new haemoproteid species, *H. caprimulgi* (Williams *et al.*, 1975) was described from the common nighthawk.

Figure X depicts the biweekly prevalence of hematozoa from non-tetraonid birds from Comox Burn during 1974. Figures XI and XII present biweekly prevalence and intensity of *Leucocytozoon* and *Haemoproteus*

Table VII. Initial appearance of avian hematozoa in 75 captive Blue Grouse chicks at Gooseneck Lake, Vancouver Island, 1973.

	Days After Exposure		
Bleeding Date	*L*†	*H*	*T*
16 July			28,* 34, 38
No. Infected	0	0	3
28 July			42, 47, 50
No. Infected	0	0	3
3 August	45, 47, 50, 54, 56	45, 45, 50	48, 51, 56, 56
No. Infected	5	3	4
Total No. Infected	5	3	10

* Number of days after exposure (chicks were exposed three days after hatching in an incubator).

† *L* = *Leucocytozoon*, *H* = *Haemoproteus*, *T* = *Trypanosoma*

Table VIII. Avian hematozoa in non-tetraonid birds from Comox Burn, Vancouver Island, 1974.

		Number of Birds Infected					
	Species	*L*†	*H*	*T*	Mf	Total	Parasite Species
Trochillidae	*Selasphorus rufus*		2			2	*H. archilochis*
Caprimulgidae	*Chordeiles minor*		2			2	*H. caprimulgi*
Picidae	*Colaptes auratus cafer*	5				5	*L.* sp.
Bombycillidae	*Bombycilla cedorum*	3				3	*L. fringillinarum/majoris*
Fringillidae	*Junco hyemalis*	1	2	2	1	4	*L. fringillinarum/majoris*
	Melospiza melodia	4	4			8	*H. fringillae/oryzivorae*
	Spinus pinus	9	7			13	*T. avium*
	Zonotrichia leucophrys		5			5	Microfilaria sp.
Parulidae	*Dendroica auduboni*	1				1	*L. fringillinarum/majoris*
	D. petechia			1		1	*H. fringillae/oryzivorae*
	Oporonis tolmei	1				1	*T. avium*
	Vermivora celata	3		1		4	
Turdidae	*Catharus guttatus*		1			1	*L. dubreuili*
	C. ustalatus		1	1		1	*H. danilewskyi*
	Ixoreus naevius	1				1	*T. avium*
	Turdus migratorius	14	1	3		14	

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Table VIII. Avian hematozoa in non-tetraonid birds from Comox Burn, Vancouver Island, 1974. - continued

		Number of Birds Infected					
	Species	*L*†	*H*	*T*	Mf	Total	Parasite Species
Tyrannidae	*Empidonax difficilis*			1		1	*T. avium*
N = 197							Double Infections
Total No. Infected		42	25	9	1	68	10
Prevalence (%)		21	13	5	0.5	34	5
Intensity†† (mean ± S.E.)		5.1 (±0.86)	26.4 (±7.94)	1.44 (±0.34)	1.0 (±1.0)	11.7 (±2.91)	32.9 (±13.8)

† *L* = *Leucocytozoon*, *H* = *Haemoproteus*, *T* = *Trypanosoma*, Mf = Microfilaria.

†† Mean number of parasites per 10,000 erythrocytes.

Figure X. Seasonal prevalence of avian hematozoa in adult and juvenile non-tetraonid birds from Comox Burn, Vancouver Island, 1974.

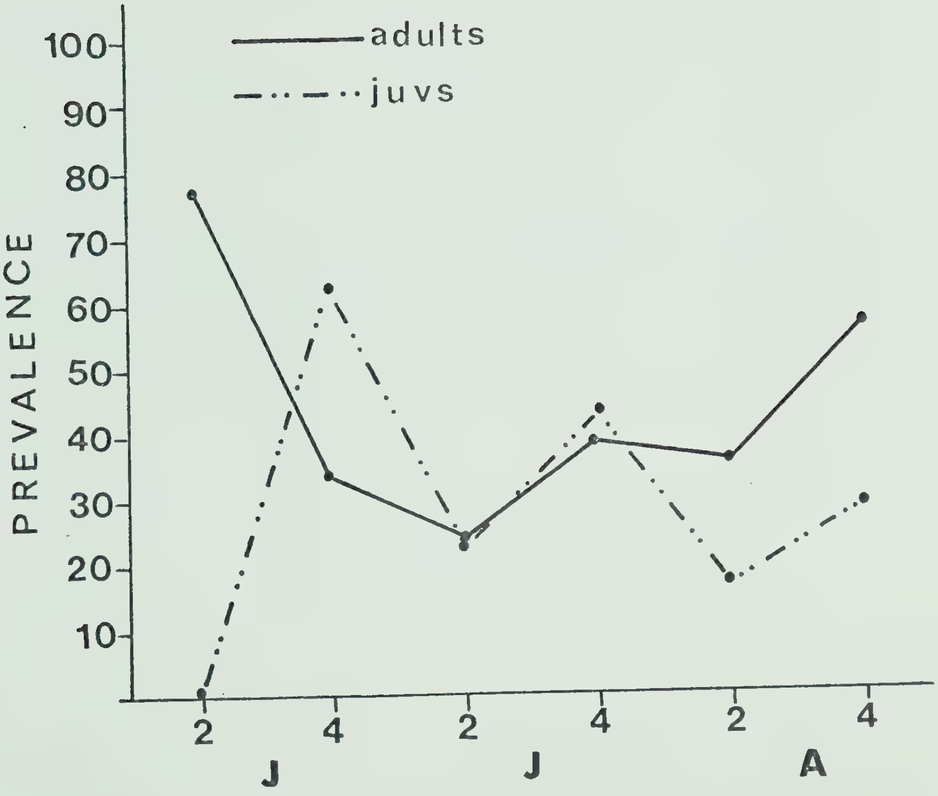
adults
juvs
PREVALENCE
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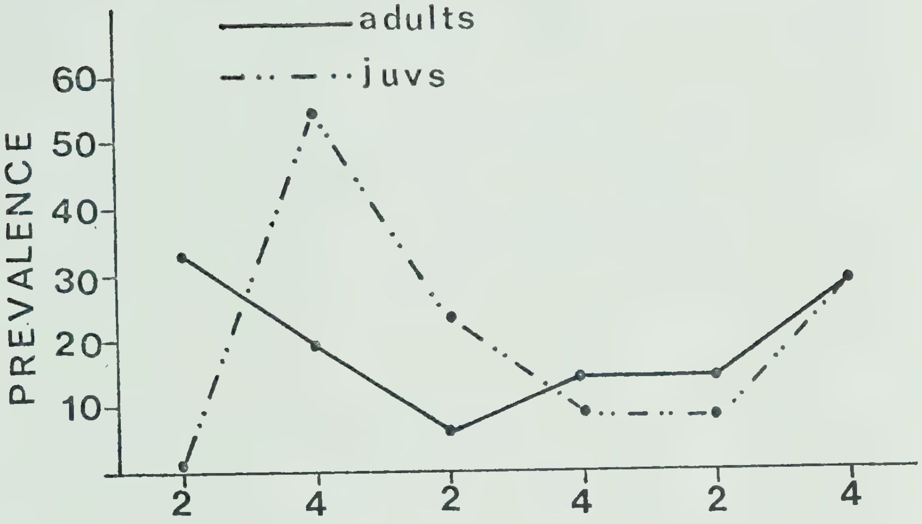
Figure XI. Seasonal prevalence and intensity of *Leucocytozoon* infections in adult and juvenile non-tetraonid birds from Comox Burn, Vancouver Island, 1974.


adults
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PREVALENCE
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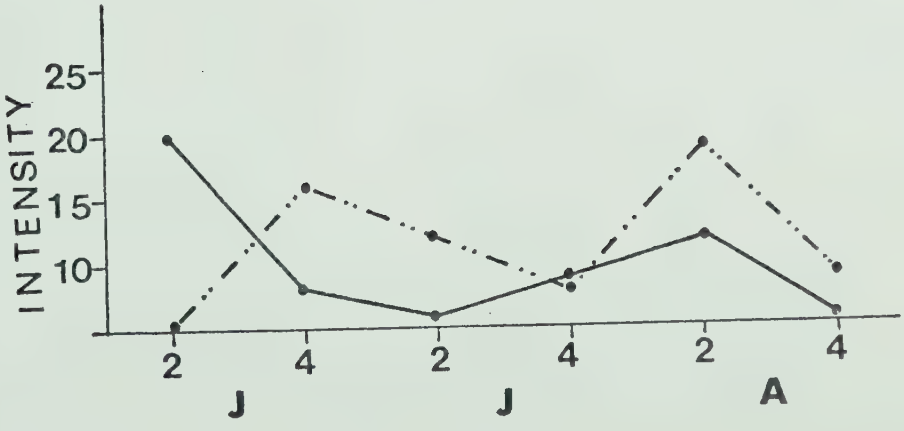
INTENSITY
25
20
15
10
2
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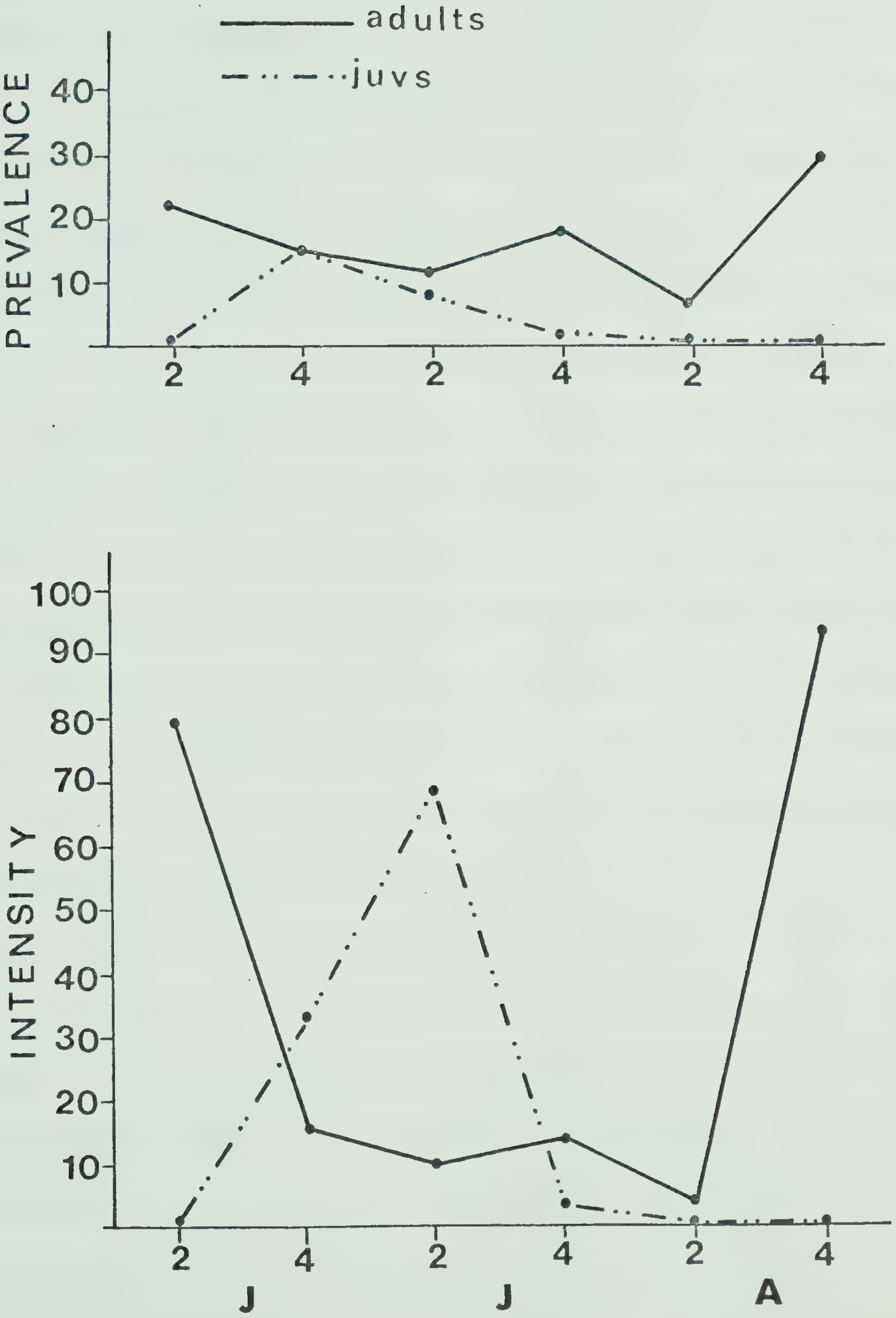
Figure XII. Seasonal prevalence and intensity of *Haemoproteus* infections in adult and juvenile non-tetraonid birds from Comox Burn, Vancouver Island, 1974.


adults
juvs
PREVALENCE
40
30
20
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4
2
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INTENSITY
100
90
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infections in adult and juvenile birds.

The major component of the avian hematozoa was composed of three or more species of *Leucocytozoon: L. fringillinarum* Woodcock, *L. majoris* (Laveran), and *L. dubreuili* M. & L., of which the first two species are thought to parasitize fringillids and several closely related passerine families and the latter, robins and other turdids. Notice that prevalence of *Leucocytozoon* infections (Figure XI) in adults is initially somewhat low, declines for the next four weeks, and then steadily increases from mid-July until examinations were terminated the end of August. The slope of the prevalence curve for adult non-tetraonids very closely parallels that of total seasonal hematozoon prevalence. The prevalence curve for juveniles, although damped somewhat, nearly mimics that for total hematozoons.

Haemoproteus infections in non-tetraonids (Figure XII) are composed of *H. archilochus* Coatney and West, *H. caprimulgi* sp. n., *H. fringillae* Labbé, and *H. oryzivorae* Anschültz. The first occurs in hummingbirds, the second in nighthawks, and the latter two both occur in fringillids and other closely related passerine families.

The majority of infections in non-tetraonids were seen in passeriform birds (89.5 percent), followed decreasingly by piciform (7.2 percent), apodiform (2.8 percent) and caprimulgiform (1.4 percent) birds. Fringillids (46.4 percent), turdids (25.9 percent) and parulids (11.4 percent) composed the major portion of infections within the passeriformes and of the entire group sampled.

ORNITHOPHILIC DIPTERA

VECTOR INCRIMINATION STUDIES: Host-baiting experiments were conducted from 5 May to 22 August, 1974, at several sites on Comox Burn. Table IX

Table IX. Percentage of infective blackflies engorged on captive Blue Grouse from Comox Burn, Vancouver Island, 1974.

Species	No. Dissected		No. Infective		% Infective
	Stomach	Salivary Glands	Sporozoites*	(Oocysts)	
Simuliidae					
Cnephia (S.) minus	5	5	0	1	0
Simulium (S.) aureum	6	6	2	1	33
Other Simuliids	38	38	0	0	0
	49	49	2	-	4

* Sporozoites are considered infective.

presents the identification of flies caught, the number dissected, and the percentage of infected (sporozoite containing) vectors. Dissections of engorged blackflies from exposed grouse proved disappointing due to the low numbers collected. Although 2 *S. aureum* harbored sporozoites of *Leucocytozoon*, and one *C. minus* and one *S. aureum* harbored oocysts, a much larger sample size is needed before definite infectivity rates can be computed. Nevertheless, circumstantial evidence indicates that these two flies are the vectors of *Leucocytozoon* in this area. Thirty-eight other engorged simuliids collected from exposed grouse harbored no parasite forms. Dissections of 37 engorged simuliids (Table X) collected in aerial sweeps near grouse revealed no developing or infective parasites.

Although the primary objective of this study was to identify those blackflies harboring *L. bonasae* sporozoites, other biting Diptera were also examined for the presence of infective parasite stages. Two engorged *Culicoides* dissected possessed oocysts in the stomach wall, presumably those of a haemoproteid. No sporozoites were found in any Ceratopogonidae.

SIMULIIDAE POPULATION STUDIES: Simuliidae larvae were quite abundant in all streams throughout both summers. Unfortunately no quantitative data was taken for the summer of 1973; however, our observations indicate that larvae were much more abundant in that year and that ornithophilic blackflies were more numerous. *S. aureum* occurred as young larvae (second instar) in late June and was present continuously until studies were terminated at the end of August. *C. minus* were first collected in streams in mid-May and were present in fair numbers until late May. Since collections tapered off quickly, it is thought that the peak of larval abundance was missed. *C. minus* was found in two streams, the majority being recovered from one stream during the middle of June. *S. aureum* larvae were collected

Table X. Species composition of adult blackflies collected from Comox Burn, Vancouver Island, 1974.

Species	Number Collected	% Total	Condition
Prosimuliinae			
Prosimulium dicum D & S	37	12.3	unfed
P. esselbaughi Sommerman	13	4.3	unfed
P. travisi Stone	102	33.7	13 engorged
Subtotal	152	50.3	13
Simuliinae			
Simulium (Eusimulium) aureum Fries*	5	17	1 engorged
S. (Hearlea) canadense Hearle	83	27.5	7 engorged
S. (Simulium) hunteri Malloch	33	10.9	13 engorged
S. (S.) venustum Say	1	0.3	unfed
Cnephia (Stegopterna) minus (D & S)*	16	5.3	2 engorged

. . . CONTINUED

Table X. Species composition of adult blackflies collected from Comox Burn, Vancouver Island, 1974. - continued

Species	Number Collected	% Total	Condition
C. (S.) mutata Malloch	12	4.0	1 engorged
Subtotal	150	49.7	24
Total	302	100	37

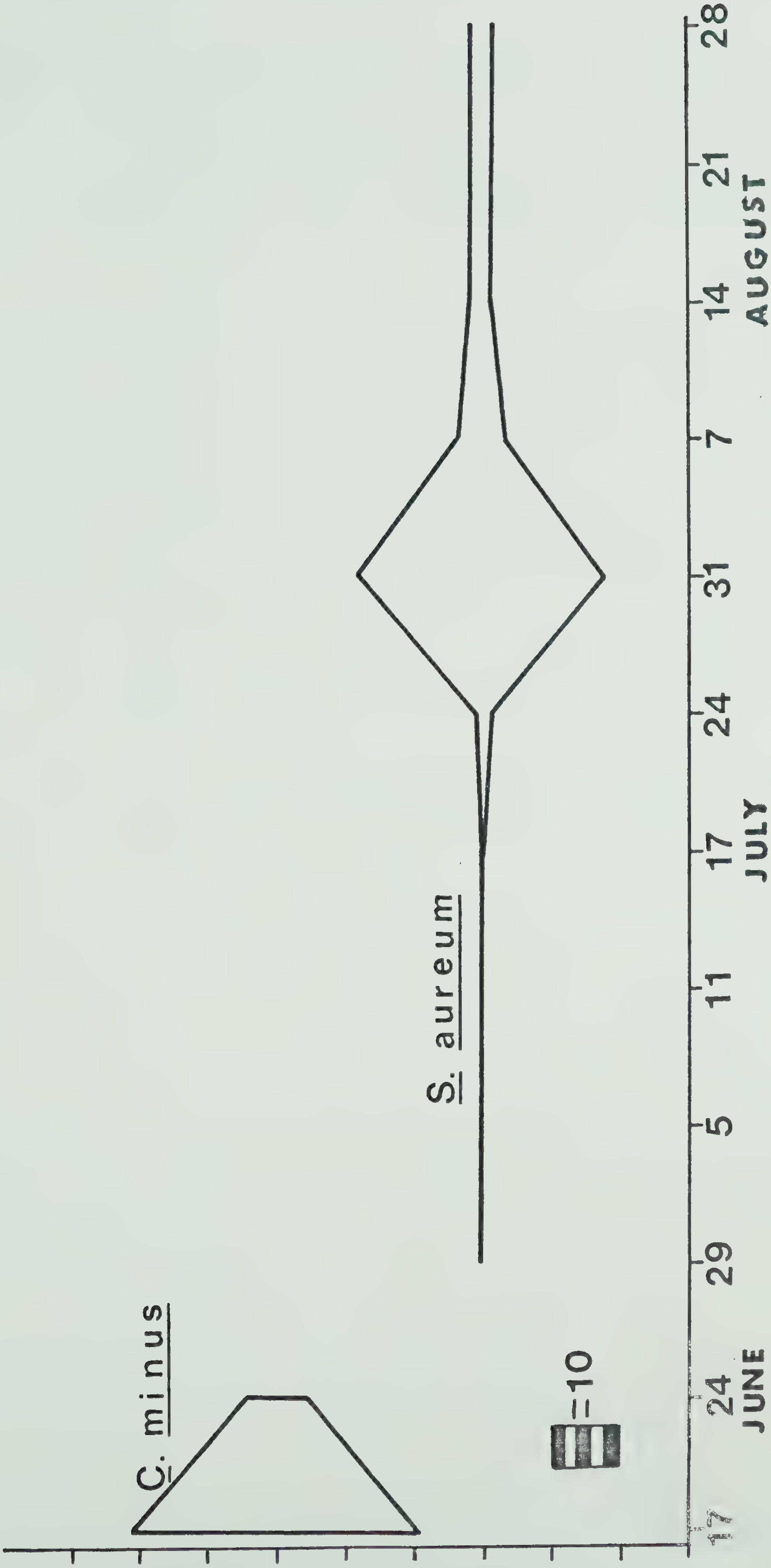
* Known ornithophilic flies.

from seven intermittent streams and were abundant from early July until the end of August. Seasonal abundance and distribution of these larvae of ornithophilic blackflies are presented in Figure XIII.

Adult blackflies listed in Table X were captured on Comox Burn from sweep-nettings near grouse. Adult *S. aureum* in this study were first collected in sweep nettings in early June and were caught throughout the summer except for a one week period in mid-July. A two week period of rains virtually extirpated a large pupal population in streams prior to mid-July. Adult *C. minus* in this study were collected from near grouse by sweep-netting in early May and were found in decreasing numbers until early July. Of the total number of adults collected, *S. aureum* and *C. minus* comprised 2 and 5 percent, respectively. No infective parasitic stages (sporozoites) were found in any of the engorged or parous flies. Both *S. aureum* and *C. minus* possess bifid claws and have been found feeding only on birds in this study. No other flies collected possessed such attributes.

Adult blackflies were found to have two feeding periods. An early morning feeding period lasted approximately 30 to 45 minutes, commencing at daylight. Although few flies were collected from exposed grouse during this period aerial sweeps yielded 15 percent of all blackflies collected. The major feeding period occurred from one hour before until thirty minutes after sunset during the summer. No simuliids were recovered after this period. Activity was highest on overcast evenings and during the calm shortly before a storm. Wind velocities over 5 mph appeared to decrease feeding activity. The most successful exposure site ("The Gallows") was situated at the edge of a douglas fir thicket, facing east, and was normally in the lee of evening breezes. Most blackflies were collected at heights

Figure XIII. Seasonal abundance and distribution of ornithophilic blackfly larvae from Comox Burn, Vancouver Island, 1974.


C. minus
S. aureum
=10
17
24
JUNE
29
5
11
17
JULY
24
31
7
14
AUGUST
21
28

between 2.5 and 5 m; a few were taken up to 6.5 m, but none were ever taken below 2.5 m. Aerial sweeps yielded more simuliids when the collector was standing atop stumps, or on knolls, and when the caged grouse was located upwind.

OTHER HEMATOPHAGOUS DIPTERA: *Culicoides* were collected from mid-July until all collections were terminated the end of August. Only one feeding period was noted, lasting from sunset onward. Most biting midges were collected at heights between 1 to 3 m. Activity ceased with any wind; all other physical factors favoring feeding activity agreed with those found influencing simuliids. Aerial sweeps were most successful when operated from the ground. Again, a grouse placed upwind yielded most of the *Culicoides* netted.

No other bird-biting Diptera were collected from exposed grouse. However, mosquitoes were collected by aerial sweeps, usually when grouse were not used as attractants. Indeed, all culicine species collected seemed to be attracted to man rather than birds, and were caught mainly after having engorged on one of the collectors. More mosquitoes were seen in 1973 than in 1974. Hippoboscids were never found on grouse, although between 50 and 75 yearlings removed from one area were examined for these flies. Only 2 louse flies were ever seen, and these were on non-tetraonids caught in mist-nets.

DISCUSSION

For the purpose of clarity in understanding the complexity of these parasite systems, this discussion will be presented in the following sequence: 1) prevalence and intensity of infections of each parasite in blue grouse and non-tetraonid birds, respectively, 2) the acquisition of blood parasites by juvenile birds (chicks), 3) the epizootiology of avian hematozoa in blue grouse and non-tetraonid birds with emphasis on *Leucocytozoon*, and 4) a conceptual model of *Leucocytozoon*, applicable to all of the parasite systems, based on the foregoing discussions. It is hoped that the complexity of *Leucocytozoon* transmission, and that of other parasites, can be reduced to a more easily visualized interaction of events.

PREVALENCE AND INTENSITY OF AVIAN HEMATOZOA

BLUE GROUSE

Blue grouse *(Dendragapus obscurus fuliginosus* (Ridgway)*)* from Comox Burn, Vancouver Island have prevalences of avian hematozoa similar to those found by other workers in that a high degree of parasitism is exhibited. This is best predicated on the basis of host-vector contact and the suitability of grouse habitat for the maintenance of adequate populations of bird-feeding Diptera capable of transmitting these parasites.

LEUCOCYTOZOON: Blue grouse from Comox Burn had significantly different prevalences of *L. bonasae* in 1973 and 1974 (Table III). This is most probably attributable to differing vector densities and infectivity rates in each year.

Since no sucking adult dipterans were found in early spring, no transmission could occur. Thus, it appears that grouse exhibit the relapse

phenomenon associated with the onset of spring and migratory habits, as found in other birds (O'Roke, 1934; Beaudoin *et al.*, 1971; Chernin, 1952; Khan and Fallis, 1970). Indeed, prevalence rates are moderately high in adult and yearling birds early in the season of both years. There is no significant difference between prevalences in each year on a seasonal basis. All adult, yearling, and most juvenile blue grouse were infected in late August. If my data are representative of the grouse population as a whole, it appears that nearly all blue grouse become infected during the first year. Juveniles (chicks), on the other hand, are presumed to be born parasite free since there is no evidence for the transfer of hematozoa from hens to offspring. This hypothesis is borne out by my data in that chicks examined shortly after hatching exhibited no parasites (Figs. I and II). This data also strengthens the evidence implicating insect-borne transmission of blood parasites to newly born juveniles.

Prevalence data for *L. bonasae* in this study differ somewhat from other studies on blue grouse. Although total prevalences vary, quite probably due to chance, combined adult and yearling, and juvenile prevalences are often strikingly similar. When adults and yearlings are combined for both years in this study a resultant prevalence of 96 percent is found. Bendell (1955) indicated that 97 percent of 169 adults and yearlings harbored *L. bonasae*. Holmes and Boag (1965) found 92 percent of 57 adults and yearlings infected, and Stabler *et al.* (1969) found 96 percent of 219 adults and yearlings infected. Prevalences in chicks for this and the above three studies are 57, 66, 67, and 35 percent, respectively.

Intensities of *L. bonasae* between years were significantly different. Female yearlings and juveniles in 1973 had significantly higher intensities

than all other groups. The factors influencing these differences are perhaps explainable on the basis of size of inoculum received from infected vectors. The depressed slopes of intensity curves of *L. bonasae* during the latter part of April in both years probably represent a return of parasite production to a level associated with chronic infections (Chernin, 1952). During mid-May, 1973, intensities in adult and yearling grouse were elevated to substantially higher peaks. Bennett and Fallis (1960) stated that high levels of parasitemia coupled with high prevalences denote active transmission. The results in this study suggest that these peaks are related to the synchronous appearance of vectors. Another peak was exhibited during early June, probably indicating a response of the parasite population to a renewed higher density of vectors. This elevated parasitemia undoubtedly provides vectors with more infective froms for the subsequent inoculation into susceptible chicks. Although intensities for all age classes in both years are statistically different, the damped curves in 1974 follow the trend seen in 1973. The factors responsible for lower intensities in all age classes of grouse in 1974 are not known. The differences may be a result of differing rates of gametocyte, zygote, oocyst, and/or sporozoite survival in the vector, a lowered differential of sporozoite survival in grouse, or a lowered superinfection rate. Huff and Marchbank (1955) found that peak oocyst production consistently preceded parasitemia peaks by 1 to 4 days with a resultant fall in oocyst numbers during a period when total numbers of parasites were still increasing. Sporozoites of *Leucocytozoon* are known to survive in birds for up to 11 days (Khan *et al.*, 1969) but their survival rate is unknown. Gingrich (1932) argued against a lowered superinfection rate, finding that acquired immunity against *Plasmodium* rendered chronically infected birds refractory

and that recovered birds were susceptible to reinfection.

Thus, three different montane biogeographic habitats produce remarkably similar prevalences. Intensity of infections, however, varies widely between the three areas. Mature birds in the first three studies possessed intensities of 17.5, 11, and 1 gametocytes per 10,000 erythrocytes, respectively. Chicks possessed intensities of 21, less than 10, and 1 gametocytes per 10,000 erythrocytes, respectively. Fowle (1944) reported that *Leucocytozoon* intensities rarely exceeded 2 per thousand blood cells and Adams and Bendell (1953) reported intensities of 1 to 2 parasites per thousand blood cells.

HAEMOPROTEUS: In 1973, blue grouse harbored significantly more infections than those in 1974 (Table IV). Weekly prevalence data for *H. canachites* indicates that yearlings of each year had significantly different prevalences. Adults and yearlings had significantly more infections than did chicks in all weeks of the season. Grouse also exhibit relapse of *Haemoproteus* as do other birds (Coatney, 1933) and adult birds exhibit this phenomenon more often than do yearlings or chicks. As a bird ages, the chances of its becoming infected are increased. Chicks in 1973 showed increasing prevalences throughout the balance of the summer. The data from 1973 differ from that of 1974 in that marked fluctuations occurred during 1974 in all age classes. Vector efficiency and success is presumed to have been very low in 1974.

Comparison of my data with that of other studies reveals major differences in prevalence. In fact, several studies (Adams and Bendell, 1953; Bendell, 1955; Schottelius, 1951) indicate that *Haemoproteus* was the predominant hematozoon found in their grouse. There was a steady increase of intensities in adults of *H. canachites* (when the one infected adult in

the first week of May is disregarded) until the latter part of July when intensities decreased somewhat. Intensities of *H. canachites* in yearlings also increased after an initial low level in the first six weeks. Intensities in chicks were characterized by a sharp increase the last week of July, coinciding with a concomitant increase in prevalence. A depressed slope of intensity value for adults at the end of April is due to low sample size (2). Sporadic depressions in both adult and yearling intensities throughout the season probably indicate that vectors of *Haemoproteus* in this area are not as efficient as their simuliid counterparts for *Leucocytozoon* transmission.

These data would suggest that moderately high prevalences are accompanied by a moderate level of parasitemia, and that lowered prevalences are characterized by increasingly high intensities. Perhaps in this way the parasite population is assured of continuance if a larger amount of infective gametocytes are present in fewer infected birds. This presupposes that availability of gametocytes is the same in each case. This is not true, unless infection confers added attractancy to the host. More information is needed to elucidate this seemingly complex relationship.

Reported intensities for *H. canachites* in mature birds are given by Fowle (1944), Bendell (1955), and Holmes and Boag (1965), and are 12 and 1 to 500 per thousand blood cells and 8 per 10,000 erythrocytes, respectively. Intensities in chicks in the above studies were noted as being always lower than those for adults and yearlings.

TRYPANOSOMA: Seasonal prevalence data for *Trypanosoma avium* infections in all age classes for each year reveal major differences. Prevalence in adults was initially high for the period mid-April to mid-May, was depressed somewhat from then until the end of July, and remained high throughout the rest of the season. Yearlings were somewhat infrequently infected until

mid-May, remained at about the 75 percent infection level through mid-summer, spiked quickly to 100 percent in mid-July and then decreased to about 65 percent for the balance of the season. It would appear that new transmission occurred during mid-June, reaching a maximum by the end of the summer. This is borne out by information provided by chick smears. Documentation of chick infections revealed a steady increasing prevalence from the end of June until mid-August. In 1974, wild fluctuations of prevalences appeared. Adults had an overall prevalence of 30 percent, yearlings of 26 percent, and chicks of 7 percent. An insignificant prevalence in adults seen the first week of May was due to small sample size. New infections appeared to be initiated in mid-July with the appearance of flagellates in adults and yearlings occurring the last week of June through the first week of July. Another increase of prevalences occurred beginning the first of August, continuing unabated until smears were no longer taken. Chicks initially caught the lag phase of parasite transmission during the first peak period (end of June) and were involved negligibly during the second transmission phase.

Comparison of *T. avium* prevalence data with that of other studies shows that grouse on Comox Burn in both years possess fewer infected individuals than is usually the case in other areas. Mature grouse from the Campbell River-Quinsam Lake region (Bendell, 1955) show higher infections (79 percent) than do Comox Burn matures (57 percent), but chicks from the former area have lower prevalences (20 percent) than from the latter (29 percent).

In 1973, chicks examined in mid-June revealed moderately high parasitemias when compared to matures during the same period. Intensities in all age classes increased the first of July to the highest of the season

and then tapered off for the balance of the season. In 1974, *T. avium* intensities in yearlings reached high levels the end of June and in mid-July, declining in the last of the summer. Juvenile intensity seemed to peak shortly after the end of July and then declined to a level equal to that of the yearlings. Little information on transmission can be derived from this figure, as the intensities are low and clumped within a narrow range.

Other studies of blue grouse hematozoa (Adams and Bendell, 1953; Bendell, 1955; Holmes and Boag, 1965) indicate that *T. avium* intensities were of the order of 1 per 10,000 erythrocytes or 1 to 20 per smear in mature and immature birds.

MICROFILARIAE: In 1973, an increase in prevalence of microfilariae in adults was noted from the first of May, which later declined and then was elevated again the middle of June. A sustained increase occurred until mid-June and then tapered off for the rest of the season. Yearlings possessed a similar sequence of peaks although the weekly prevalence values were usually 15 to 40 percent lower. Chicks in 1973 were found to harbor microfilariae when examined in mid-June, even though the prepatent period has been found to be 2 months (Gibson, 1965). This would indicate that the chick was exposed to vectors at least by the third week of May, a date one week prior to normal initiation of hatching. That such contact could occur that early in the year is rare, unless the prepatent period is shortened by one to two weeks by favorable circumstances within the host. There is currently no proof to substantiate this line of thought and the early occurrence of microfilariae in chicks remains an enigma.

In 1974, grouse had no detectable microfilariae in the blood until the first week of May. Adults showed a bimodality of prevalence: the

first in mid-May and the second during the first week of August. Yearlings maintained relatively lower prevalences throughout the season except for a rapid increase in mid-June. Chicks showed infections only during mid-August, a reasonable amount of time for developing larvae to occur. It would therefore appear that transmission to chicks occurs early on in their life.

Other workers (Table I) have found different degrees of prevalence in blue grouse but have rarely commented on the degree, or level of infections. Gibson (1965) found that *Mf*. sp. B. were significantly more prevalent in adult males than females or in yearlings. In the present study, this was true only for adult males and females in 1973.

No figures are presented for weekly microfilariae intensities due to the low order of magnitude. Suffice it to say that adults maintained an average of 3.1 and 1.2 microfilariae for 1973 and 1974, respectively; peak intensity was found to occur during the periods late May to mid-June in 1973 and late June to early July in 1974. Yearlings in 1973 and 1974 followed the same trends for each respective year, possessing 2.6 and 1.8 larvae per 10,000 erythrocytes. Chicks were infrequently encountered with more than 1 larvae seen during routine examinations. In this study, significantly different intensities occurred only between adult males, yearling males, and yearling females of each year.

NON-TETRAONID BIRDS

The biweekly prevalence of hematozoa in adults and juveniles (Figure X). were quite different in 1974. As expected from information gleaned in other studies of this nature (Box, 1966; Manwell, 1955a; Mohammed, 1958) adult prevalences were highest at the beginning of the summer. A depressed

prevalence followed, during which time gametocytes were often reduced below the threshold detected by the examination. An increase in prevalence was associated with the end of the season and the concomitant appearance of numerous bird-biting dipterans. A large portion of the juveniles sampled were infected the last week of June. They later exhibited a lowered prevalence as increasing greater numbers of uninfected fledglings were added to the population. Note, however, that the slope of the juvenile prevalence curve closely parallels that of the adults during the latter half of August. Both age classes of the population presumably responded to a higher level of parasite transmission.

LEUCOCYTOZOON: Intensity data for *Leucocytozoon* infections in non-tetraonids generate curves with slopes closely approximating prevalence curves for adults and fledglings. However, toward the latter half of the summer, intensities for both age classes declined. An increased number of uninfected fledglings was introduced into the population at this time; in effect, diluting the number of infectives available to vectors. The factor responsible for the decreased intensity in adult birds during the end of the summer is thought to be a lowered production of gametocytes, characteristic of a long-standing, or chronic, infection (Beaudoin *et al.*, 1971; Bennett and Fallis, 1960).

HAEMOPROTEUS: The prevalence of *Haemoproteus* infections in adults gradually decreases until mid-August when an upsurge occurs, peaking higher than the initial value. Juvenile prevalence curves increase to the 15 percent level at the end of June and then gradually decline until no fledglings are infected by the first of August. *Haemoproteus* transmission, therefore, must occur before the end of June for gametocytes to appear in the peripheral

circulation. High intensity values for adults correspond to high prevalence levels, indicating new transmission (Bennett and Fallis, 1960), as do high juvenile intensities. It is interesting that peak intensity in juveniles occurs two weeks after the highest prevalence.

TRYPANOSOMA: Trypanosoma avium occurs in 13 percent of the infected non-tetraonids, in 14.5 percent of the infected adults, and in 9.5 percent of the infected juveniles. Infections were found from the end of June to early August in adults and during late July in juveniles. Intensity in adults ranged from 1 to 2.5 in adults and was 1 per 10,000 erythrocytes in juveniles.

MICROFILARIAE: An unidentified microfilaria was found in a juvenile dark-eyed junco during the first of August and none were seen in smears from any other non-tetraonid.

Robins (20.3 percent), pine siskins (17.4 percent) and song sparrows (11.6 percent) were the predominantly infected species, unsurprisingly, since these birds nest and feed in open grouse habitat and are, therefore, more available to vectors. Juncos and white-crowned sparrows also occupy the same habitat and were infected at slightly lower levels (8.7 percent and 7.2 percent, respectively). Birds nesting and feeding at the borders of the burn and in willow swales on the burns (parulids, flycatchers (1.4 percent) and kinglets (0 percent)) are less available and quite clearly exhibit a lower infection rate. Birds residing in dense thickets and mature forests rarely show infections, due to the inherent difficulties in finding them on the part of the vectors. However, nighthawks, a species known to nest in exposed areas, rarely exhibit demonstrable parasitemias. This is very likely related to the feeding habit of the vectors (they

rarely occur near the ground) and to the hosts' feeding habits (they hawk for insects late in the evenings at relatively high heights). Nighthawks are immobile for most of the day at a time when vectors very infrequently sally forth. Hummingbirds, of which only 2 were found to be infected, are very active during the day and undoubtedly present few opportunities for vectors to engorge. At night they rest in a torporous state; at this time *Culicoides*, due to their preferred nocturnal feeding periods, are temporally distributed to take advantage of these small birds. It is interesting to note that 5 of 6 flicker chicks were infected, prior to fledging. They were situated deep within a crevice of a charred douglas fir stump, 10 m above the ground. This suggests that the simuliid vectors of these *Leucocytozoon* infections were quite disposed to seeking out "enclosed" prey at heights normally thought to be above their activity range. Bennett (1960) indicated that more engorged sylvan diptera were collected at heights between 3 and 7 meters above ground, but rarely occurred above the upper limit. Anderson and DeFoliart (1961) found that *Simulium aureum* exhibited a marked aerial stratification but was never collected from avian bait above 7 meters. It is unlikely, but not impossible, that adult flickers, returning to feed their young, transport partially-fed vectors back to the nest site.

Comparison of the prevalences of terrestrial non-tetraonid birds from other North American surveys revealed that Comox Burn prevalences were not statistically different from the total average prevalences. Table XI tabulates results reported in 37 major surveys, of which all include most of the same species and families examined in this study. Comox Burn birds were infected at the 34 percent level; this favorably compares to the mean prevalence of the other studies combined (38.4 percent). The

Table XI. Major North American surveys of avian hematozoa.

Author	Date	Locality	Number Examined	Prevalence (%)	Number of Species
Opie and MacCallum†	1898	MD, Canada	125	12.8*	6
Manwell and Herman	1935	NY, MA	652	8.3*	34
Coatney and Roudabush	1937	NB	89	29.2	44
Wood and Wood	1937	CA	203	4*	21
Coatney	1938	IA	63	11.1*	23
Coatney and West	1938	NB	84	22.6	35
Herman	1938	MA	2384	8.8*	61
Herms *et al.*	1939	CA	150	27.3	30
Huff	1939	IL	967	27.4	81
Coatney and Jellison	1940	MT	22	40.9	4
Wetmore	1941	DC, MD	618	30.4	53
Wohnus and Ryerson	1941	CA	130	41.5	22
Jordan	1943	GA	1103	14.1*	24
Thompson	1943	GA	275	20*	23
Wood and Herman	1943	Southwest USA	1525	23.4*	112
Wirth	1944	LA	63	3.2*	30
Clarke	1946	ONT	111	34.2	54

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Table XI. Major North American surveys of avian hematozoa. - continued

Author	Date	Locality	Number Examined	Prevalence (%)	Number of Species
Hart	1949	SC	387	59.7*	17
Hunninen and Young	1950	SC	737	27.5	21
Couch	1951	TX	434	52.5*	17
Sachs	1953	IL	158	21.5*	15
Love *et al.*	1953	GA	1246	25.8*	97
Manwell	1954	CO	82	32.9	9
Manwell	1955a	NY	1037	29.1	17
Manwell	1955b	NY, CO	60	67*	1
Bennett and Fallis	1960	ONT	3004	49.7*	94
Farmer	1960	IA	568	17.4*	13
Laird	1961	NWT	159	0*	23
Al-Dubagh	1964	OH	284	21.5*	13
Clark and Swinehart	1966	CA	383	34.9	23
Collins *et al.*	1966	SC	603	22.7*	67
Marx	1966	MI, WI	237	10.5*	36
Clark	1967	WA	124	73.4*	1
Smith	1967	OH	92	50	16
Stabler and Kitzmiller	1970	CO	1361	50.9*	101

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Table XI. Major North American surveys of avian hematozoa. - continued

Author	Date	Locality	Number Examined	Prevalence (%)	Number of Species
Bennett	1972	LABR	454	37.7	38
Bennett *et al.*	1974	NFLD	2675	69.9*	56
Total	N = 37		22,649	38.4	36.1
This Study	1975	BC	197	34	28

† Studies combined.

* Statistically different ($P < 0.01$) prevalence from the present study.

number of avian species examined in this study represents slightly more than two-thirds of the average number of species listed in the other studies. Several studies which were of wider scope than this study (more orders and families), but which included families similar to the present study were analyzed for selected prevalences. Galindo and Sousa (1966) and Huff and Wetmore (1967) surveyed 249 and 119 species of 19 and 13 orders, respectively. When prevalence data on infections in passeriform, piciform, caprimulgiform, and apodiform birds are tabulated for the former study, a prevalence of 14.9 percent is noted. Similar data is not extractable for Huff and Wetmore's data but they related that all *Plasmodium* and microfilarid infections occurred in passerines, that *Haemoproteus* infections were seen only in 7 passerine and 1 picid families, and that *Leucocytozoon* infections were not found in any of the preceding. It is also interesting that these surveys were done in Panama and that many species found breeding in northern latitudes of the continent migrate through Panama for the winter. It thus seems that parasites are lost or gametocyte production is depressed during this period.

Canadian surveys usually provide prevalences higher than that found on Vancouver Island. Studies from Ontario indicate a prevalence of 50 percent; that from Newfoundland, 70 percent. Comparable species were examined in all three areas. These differences in prevalence will probably be explained on the basis of vector density and/or efficiency of transmission.

Prevalences of blue grouse and non-tetraonid hematozoa of all genera are significantly different. It can be postulated that differences occur due to one or more of the following factors: 1) blue grouse are inherently more attractive to vectors, the vectors being highly specific, 2) grouse

are more abundant than non-tetraonids, 3) grouse are dispersed in areas in which they are more available to vectors, or 4) the habits of non-tetraonids render them less available to vector contact. Evidence for the first postulate is presented by Anderson and De Foliart (1961) who stated that certain ornithophilic species exhibited host preferences within a given habitat. Bennett (1960) collected more *S. aureum* feeding on ruffed grouse than the total collected from 9 other species of birds in Ontario. Limited observations during the present study indicate that simuliids are more readily attracted to wild grouse than to passerines caught in mist-nets. Evidence for the second hypothesis is lacking. Zwickel (1972) indicated that approximately 473 male and female adults and yearlings resided in the combined 1500 hectare study area. A slowly increasing population has been noted since that estimate was made (Zwickel, personal communication). The total number of non-tetraonids in the study area far outnumber grouse since Martin (1973) found 1 breeding pair of robins per 5.5 hectares on a 184 hectare portion of the study area. If this is indicative of the true population, a conservative estimate would place roughly 200 breeding pairs of robins on the study area. Sparrows and warblers are as common throughout the area as are robins. Therefore the non-tetraonid population is more dense than that of grouse. Support for the third hypothesis exists from numerous observations throughout both years on habitat preferences of most birds. As described previously, many passerines occur concurrently in the same areas as grouse, although feeding habits may stratify them. Other birds nest in very dense vegetation, some feeding within these areas and others without. Warblers, flycatchers and thrushes belong to this latter category. The highest prevalences were found in robins and other passerines which were located on the open

burns. Moreover, their rates of infection were significantly lower than that found in grouse. Therefore, grouse must come into contact with vectors more often in these areas than do non-tetraonids. Vector feeding preferences based on stratification of the host most certainly influence the prevalence of infections noted. This explanation, in part, applies to the fourth hypothesis. Additionally, host feeding periods (nighthawks) may preclude them from contact with vectors. Downes *et al.* (1962) suggested that vector response to host color, chemicals, size, shape, and movement predicates host-finding efficiency and, therefore, the contact between host and vector so necessary for parasite transmission. Studies on host preferences of flies are indicated; as well, it would be useful to determine if grouse are more susceptible to blood parasites than their passerine counterparts and the effect of biomass on host attractancy.

ACQUISITION OF HEMATOZOA BY BLUE GROUSE

The period of time when juvenile blue grouse acquire hematozoon infections influences the prevalence of parasites in the survivors of that age class the following year.

Leucocytozoon bonasae appears in the peripheral circulation as gametocytes approximately 12 to 14 days after an infective fly has inoculated a susceptible bird. Observations made during 1973 on 75 captive chicks provide a basis for comparison with wild populations. Gametocytes of *L. bonasae* were seen in smears of 5 chicks 40 to 51 days after exposure. It is possible that infective flies obtained their infections from ruffed grouse resident in adjacent alder habitat since blue grouse habitat was 8 km distant. Naturally occurring grouse chicks first exhibited gametocytemias the first

week of July, 1973. Approximate chick ages were obtained by back-dating (Zwickel and Lance, 1966), utilizing primary feather growth patterns. Juveniles infected during this period were found to be 3 to 4 weeks old. Therefore, infective flies must have fed on them shortly after the young were hatched. Young grouse are known to be primarily terrestrial for the first week of life, and are capable of 60 m flight only after the second week (Zwickel, 1967). In 1974, chicks were first found to be infected the second week of July. Although hatch dates were similar for both years (Zwickel, personal communication), chicks in 1974 lagged one week behind their counterparts the previous year in acquiring infections. By the end of both summers, 84 percent of each juvenile population was infected. It should be made clear that hens often renest if the first nest has been disturbed or depredated. Renesting often protracts hatch dates until the third week of August. Therefore, one can envision broods hatching continually from early June until mid-August. With this in mind, one should realize that, although 84 percent of the population may be infected, other individuals may not as yet exhibit any gametocytemia due to the prepatent period required.

Haemoproteus canachites infections were first detected in captive chicks in 1973 40 to 45 days after exposure. Wild juveniles first exhibited parasitemias in 1973 the last week of June. Again most of the chicks were 3 to 4 weeks of age and infection must have occurred a few days after hatching. It is notable that a lower prevalence of *H. canachites* infected chicks occurred in 1974; indeed, infections were not noticed until the first week of August. It is very probable that climatic conditions precluded large populations of *Culicoides* during 1974, since larval habitat requirements are restricted. Nevertheless, gametocyte intensity levels in

1974 far exceed those recorded in 1973. Unless a higher mean intensity confers added attractancy to a host, it is doubtful that high intensities would offset low prevalences in some years, since the number of uninfected hosts available would prove a barrier to vector efficiency.

Trypanosoma avium infections were first recorded from 3 captive grouse chicks 23 to 38 days after their initial placement in the aviary. A number of chicks were always found infected during each of the three examination periods. A total of 10 chicks were infected during the period 23 to 51 days after exposure during 1973. Wild chicks in 1973 were first found infected the last week of June and prevalence rates gradually increased throughout the summer. The second week of July, 1974, marked the first demonstrable *T. avium* infections in chicks. Overall prevalences were much higher in 1973 than in 1974, as were overall intensities. Woo (1964) found trypanosomes in the circulating blood 48 hours after inoculating "clean" grouse chicks with 10 day old cultured metacyclic *T. avium*. No attempts were made to infect "clean" chicks by infective vectors. It would seem, therefore, that natural infections require 2 or more days for trypanosomes to become present in the peripheral circulation. Chicks examined in late June 1973 were 2 to 4 weeks of age and could theoretically have acquired *T. avium* infections less than three days before examination.

Microfilariae were not detected in 1973 in captive grouse chicks. In wild chicks, however, microfilarid larvae were found as early as the third week of July. As previously pointed out, a prepatency of 2 months is thought to be required (Gibson, 1965). It would appear that any chick with such an early infection must have been infected at the earliest hatch date. Infections in 1974 were not seen until mid-August. Vector efficiency during this year must have been low or transmission must have been delayed.

It is not known when or where uninfected adult and yearling grouse acquire infections during any year. Only recapture of known birds with known infection levels will reveal the complexities surrounding infections in subsequent years. It is probable that the maintenance of a parasite-free status decreases with the amount of time an animal is available to infective vectors.

EPIZOOTIOLOGY

The assorted facts and conclusions concerning the biology of hematozoa, their tetraonid hosts and their dipteran vectors which were previously discussed independently are here considered in relation to each other. Since much of the field research involved *Leucocytozoon bonasae*, blue grouse, and simuliids on Vancouver Island, this complex will be considered in greatest detail; other hematozoa, hosts, and vectors will be brought into the picture for discussion.

BLUE GROUSE

LEUCOCYTOZOON: When the grouse descend in spring from the winter range to their breeding areas on the reforested lower slopes, most of the adults and yearlings harbor infections of *L. bonasae*; many carry double infections. During the period when territories become established and nesting sites are selected, it is unlikely that hematozoa transmission occurs, because few ornithophilic dipterans are emerging and ambient temperatures over extended periods may be below the minimum necessary for development of blood parasites in intermediate hosts.

By late May populations of biting flies are increasing, and grouse-biting simuliids are composed of *Cnephia minus*. Daytime temperatures are

still moderately low (therefore sporozoite development would require several weeks) and transmission is probably negligible before early June.

In early June air temperatures rise and populations of *C. minus* and *S. aureum* increase markedly, thus greatly enhancing the transmission potential of *L. bonasae*. The next three weeks are probably the most favorable for transmission of this species to adult and yearling males.

When chicks enlarge the host population, the probability of vector-host contact is increased, but concomitantly, the probability of vector-uninfected host contact is greatly increased. The success of leucocytozoid infection of newly hatched grouse chicks should be strongly influenced by the degree of synchrony between peak abundance of vectors and peak hatching of chicks. Two types of synchrony can be envisioned. Type A: Most of the chicks hatch before vectors are numerous. In this case, as flies become abundant many newly emerged individuals of the vector species will be feeding on uninfected grouse. The ratio of infected to uninfected vectors will be moderately low. Therefore, correspondingly few chicks will become infected early. Type B: Most of the chicks hatch after the vectors have been abundant for several weeks. The ratio of infected to uninfected vectors will be considerably higher than in the previous case, and, consequently, a correspondingly greater proportion of the chicks should acquire infections early.

At first glance, the relationship of vector to young chick in the transmission of *L. bonasae* in 1973 seems to be of Type B synchrony. *C. minus* and *S. aureum* have been abundant for upwards of a week before the chicks hatch, and have had sufficient time to feed on infected adult or yearling grouse. Sporozoite development in simuliids probably requires 7 to 10 days at the temperatures of early to mid-June (Fallis and Bennett,

1962); therefore, one would expect infective inoculum to be present in the blackflies when most of the chicks are newly hatched. Many chicks should become infected after a few days of hatching. *Leucocytozoon bonasae* gametocytes were not detected in blood smears of captive juveniles until, at the earliest, 45 days after hatching. A few wild juveniles possessed gametocytes roughly two weeks after hatching was initiated, although the majority of chicks were not infected until the end of July, 2 to 3 weeks after the peak of hatching in the Comox Burn area.

Infection in chicks in 1974 appear to follow a different pattern. Climatic factors retarded the peak of biting Diptera for roughly two weeks. After this period of time, uninfected chicks were quite abundant and a Type A synchrony seemed to take place. Yearly differences in the peak hatching of chicks caused by environmental factors and/or the delaying of emergence of adult simuliids could presumably alter the types of synchrony outlined above. Eighty percent of all chicks in the Comox Burn area hatch between the second week of June and the second week of July, depending on elevation.

The following related aspects of the habits of chicks and of vectors probably result in minimal vector-chick contact during June: 1) Until they are about two weeks old, chicks are incapable of efficient flight and are by necessity terrestrial, but *S. aureum* and *C. minus* are much less abundant at ground level than in trees; 2) Chick activity commences each day when direct sunlight evaporates the dew and the air temperature rises (Zwickel, 1967), but by this time simuliid activity has declined from its early morning peak.

The presence of *L. bonasae* in a few chicks in early July undoubtedly indicates that some simuliid-chick contact occurs before the grouse are

one month old. Perhaps much of this is a result of egg-laden female simuliids passing low over grouse range to oviposit in the streams; spatial contact would thus be increased. Vector-chick contacts in this period may occur in the late evenings, when temperatures are still elevated and blackflies are active. Mild, overcast days may provide the most favorable conditions for transmission, since simuliids tend to drop near the ground during the day and become active in cloudy weather. These limited observations seem to agree with the findings of Wolfe and Peterson (1958, 1960), Bennett (1960) and Anderson and DeFoliart (1961).

Since *C. minus* is continuously present, though as a low population, throughout most of July, this species is likely responsible for mid-summer transmission to the rapidly growing chicks. In early August a resurgence of *S. aureum* occurs. Despite its low density, there are several reasons for believing that this population is responsible for considerable transmission of *L. bonasae*. 1) *S. aureum* is the predominant species feeding on grouse at this time. 2) Air temperatures are high; development of sporozoites to the infective stage requires less than a week. Other workers (Fallis and Bennett, 1958) state that *S. aureum* is a highly efficient intermediate host, capable of supporting large numbers of sporozoites.

Some adult male blue grouse are present on the range when the resurgence of *S. aureum* begins; however, by mid-August virtually all have departed for the montane wintering grounds. This means that early in August the newly emerged blackflies probably acquire inoculum from cocks as well as hens, but later, only the chicks and hens are available to receive infective sporozoites.

The higher prevalence of *L. bonasae* in adult males than in adult females or in yearlings (most of which could have acquired their infections

only as chicks) is most easily attributed to the relative availability of these groups to infective vectors. Adult males may be the most frequently attacked by simuliids because much of their daily activity while vectors are abundant is restricted to "hooting" sites in which they are readily accessible to infective vectors. In the high grouse populations on the open "burns," male territories are rather small and frequently are contiguous; "hooting" sites are often associated with slight elevations and young douglas firs (McNicholl, personal communication), and the area occupied by grouse is relatively homogeneous. These areas bear few obstructions to the movement of vectors. Yearling males on the breeding range are usually found wandering through the territories of the cocks; as a result they likely encounter pockets of infected vectors.

The lower prevalence of *L. bonasae* in adult hens than in adult cocks may be related to the lengthy incubation period (26 days) during most of which the hens are restricted to their terrestrial nests. Females leave the nest only during pre-daylight hours to defecate and feed. The rest of their time is spent incubating. Results of several studies indicate that the differential prevalence of hematozoan infections may reflect factors other than differential availability to definitive hosts. Wolfe and Peterson (1960) found that in the morning and evening, light-skinned people were bitten more frequently than those with dark coloration, whereas during the day the opposite was true. Fallis and Smith (1964) provided convincing evidence that some ornithophilic simuliids are strongly attracted to their hosts by chemical olfactory stimuli. Bradbury and Bennett (1974) have shown that simuliids have a marked ability to discriminate between targets during near orientation on the basis of color, independent of the amount of CO_2. Simuliid vision was effective between 0 and 180 cm downwind

from a fixed target. It would indeed by profitable in the future to investigate whether differences in pigmentation, size and physiologic state which exist among cocks, hens, and chicks result in different "attraction potentials" for simuliids, and if so, to what extent these influence the transmission of *L. bonasae.*

Downes *et al.* (1962) indicates that the pattern of blackfly dispersal in relation to population size could determine the rate of parasite transmission. By the time the population has aged sufficiently to consist largely of old flies, these exist in large numbers only close to the breeding stream. It is presumed that old flies disperse more slowly than young ones. Thus the probability of infective bites decreases rapidly with distance from the stream; the scale of the pattern would vary with the population size and the dispersal habits of the species. It would, therefore, prove of much interest to monitor the parasitemias of territorial cocks near streams and those more distant to reveal if, indeed, the above hypothesis is true.

HAEMOPROTEUS: Transmission of *H. canachites* to chicks probably occurs from early July until mid-August, since *Culicoides* are present on the grouse range during this period. Radical climatic extremes were common during 1974 and they very likely adversely influenced the vector population. Since no hippoboscids were collected from grouse, and since *Culicoides* were often seen hovering over and on grouse, it is presumed that *Culicoides* are the vectors of *H. canachites.* Two of fifteen *Culicoides* dissected possessed oocysts. Fallis and Bennett (1960) incriminated *L. sphagnumensis* as vectors of *H. canachites* to ruffed and spruce grouse in Ontario and indicated that other workers would find *Culicoides* to be vectors of this

parasite elsewhere. *Culicoides* populations would be subject to adverse stress under conditions of fluctuating ambient temperatures, and alternating wet and dry periods, as was the case in 1974.

Many of the same factors which influence *L. bonasae* no doubt affect transmission of this species. *Haemoproteus canachites* occurs less frequently than *L. bonasae* in adults of either sex and in both total yearlings and adults. One might expect this to be the case for the following reasons: 1) the moderately small vector population for *H. canachites*, 2) the use of one, rather than two, daily feeding periods by *Culicoides*, 3) the greater suppressant effect by wind on *Culicoides* activity and 4) the longer developmental period (7-14 days) of *H. canachites* in its intermediate host. The following aspects of *Culicoides* biology may mitigate against some of the negative influences by favoring vector-host contact: 1) the tendency for *Culicoides* to feed in moderate numbers at ground level where most of the activities of the host take place, 2) prolongation of the feeding activities of *Culicoides* after nightfall, when grouse are roosting on the ground or in young douglas fir trees, motionless, and therefore easily attacked, and 3) continuous presence of the vector population during the summer.

TRYPANOSOMA: Transmission of *T. avium* to grouse chicks probably occurs from early July until mid-August, since simuliids seem to be the vectors involved (Bennett, 1961, 1970a) in the northern portion of the Western Hemisphere. Again, many of the same factors influencing *L. bonasae* transmission to chicks are responsible for this parasite's transfer. There appears to be little preferential occurrence between the sexes of adults and yearlings. If *L. bonasae* and *T. avium* utilize the same vector

species for their transfer, one is immediately aware of disparencies in prevalence data. This may be explained in the following manner: 1) some interspecific physiologic inhibition by *L. bonasae* may be occurring which tends to depress, to a degree, the development of flagellates within the fly, 2) *T. avium* may experience difficulties in penetration of the vector's peritrophic membrane, thus reducing the number of flagellates produced, and 3) simuliids may be more suitable intermediate hosts for leucocytozoid development than for trypanosomes. The possibility that mosquitoes may vector trypanosomes, in the absence of experimental data, cannot be dismissed. That trypanosomes do not reproduce in vertebrate hosts certainly affects the probability of their being picked up by the vectors.

MICROFILARIAE: Transmission of microfilariae probably occurs during mid-June until early August. Larvae of *Microfilariae* sp. B. are not present in routine blood film examinations until the second week of July. *C. minus* is probably responsible for its transmission during mid-summer; *S. aureum* undoubtedly is responsible for its transmission during the latter part of the summer, after an early August resurgence occurs (Gibson, 1965). There is little difference of microfilarial prevalences between sexes of adults or of yearlings. However, total adults are more frequently parasitized by this nematode larvae than are the total yearlings. Factors contributing to the transmission efficiency of *Mf*. sp. B. are most probably similar to those affecting *L. bonasae* transfer.

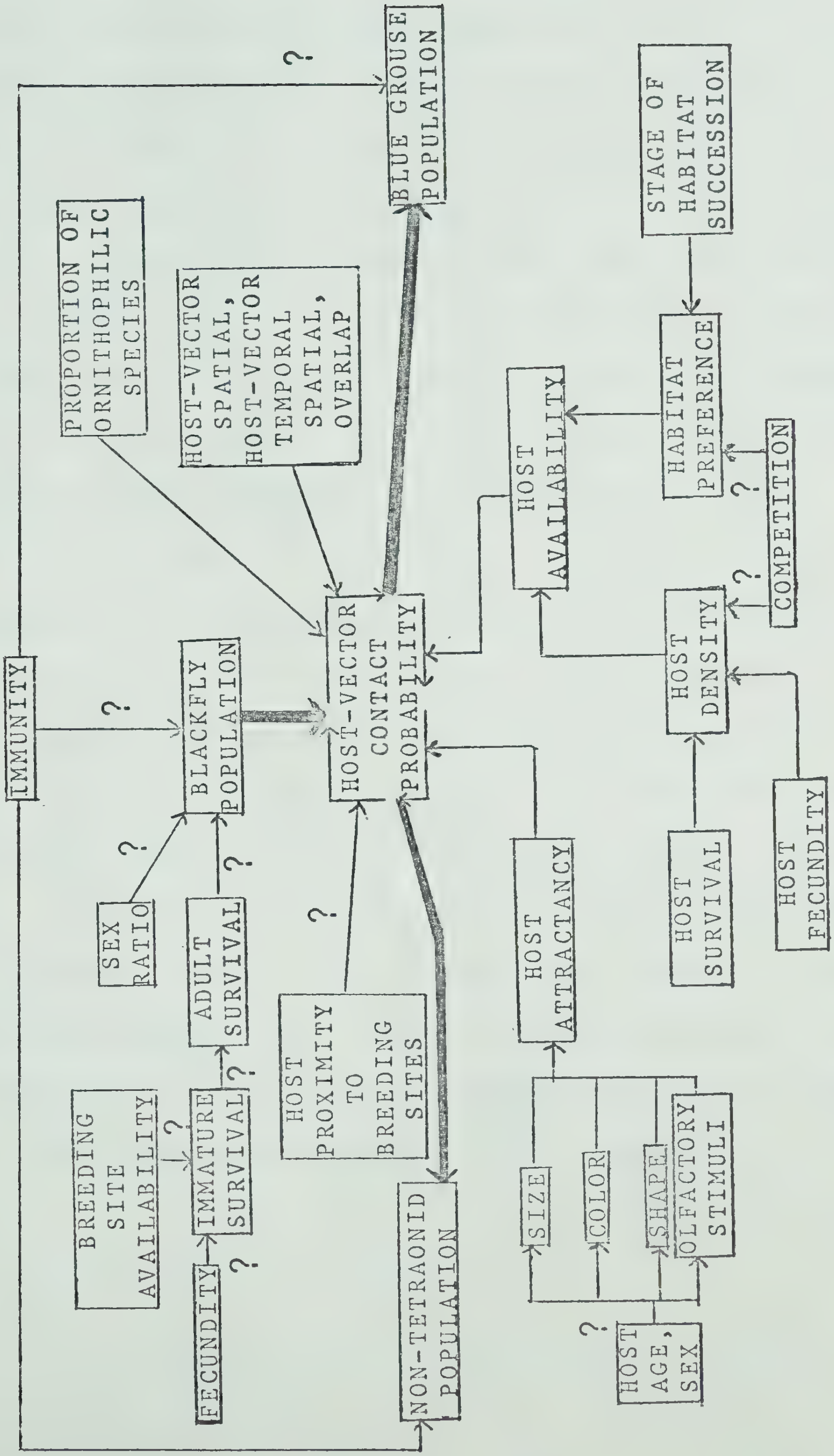
NON-TETRAONID BIRDS

The frequently arboreal habits of passerines and other species of non-tetraonid birds would seem to predispose them to high rates of

hematozoon infections, yet relatively few infected birds were found (Table VIII). If we assume that the sample examined was indicative of hematozoon prevalence in small passerines, transmission failure is probably a function of the isolating effect of their habitat, their relatively lower population density on "open burns" and the existence of Type A vector-chick synchrony. Vector-host contact is probably less frequent in dense willow and alder swales which the majority of these birds occupy than on adjoining "burns," and flies carrying infective inoculum may be filtered out near the periphery. Indeed, those birds feeding and/or nesting in the open burns (robins, song sparrows, juncos, and siskins) are more often infected than those occupying sylvan and border habitats. This may, in part, be due to differences in host biomass, the filtering effect of dense vegetation on vector seeking ability, or cryptic pathogenesis.

MODEL OF *LEUCOCYTOZOON* INFECTIONS: Avenues of future research are often best presented in model form. Figure XIV depicts the interacting factors thought to influence the *Leucocytozoon*-blackfly system in various species of birds from Comox Burn, Vancouver Island. With modifications for life cycles, this scheme should apply to other hematozoa-vector systems. Those factors investigated by various authors are indicated by a solid line; those still unknown, by a question mark. Although the prevalence and intensity of infections in blue grouse have been documented by various workers over the last thirty years, it is desirable to continue monitoring these parameters in the future. Much information can be gained from recapture information on known banded birds. Specifically, the proportion of grouse exhibiting relapse of parasite infections should be investigated. The factors influencing this renewed production of infective parasite

Figure XIV. Model of factors affecting *Leucocytozoon* infections.


IMMUNITY
BLUE GROUSE POPULATION
PROPORTION OF ORNITHOPHILIC SPECIES
HOST-VECTOR SPATIAL, HOST-VECTOR TEMPORAL SPATIAL, OVERLAP
STAGE OF HABITAT SUCCESSION
HABITAT PREFERENCE
HOST AVAILABILITY
COMPETITION
BLACKFLY POPULATION
HOST-VECTOR CONTACT PROBABILITY
HOST DENSITY
SEX RATIO
ADULT SURVIVAL
HOST PROXIMITY TO BREEDING SITES
HOST ATTRACTANCY
HOST SURVIVAL
HOST FECUNDITY
BREEDING SITE AVAILABILITY
IMMATURE SURVIVAL
FECUNDITY
NON-TETRAONID POPULATION
SIZE
COLOR
SHAPE
OLFACTORY STIMULI
HOST AGE, SEX
?

forms are almost wholly unknown. Recapture information will allow the true seasonal fate of infections in various cohorts to be known. Investigation of differential immunity between blue grouse and other birds should be explored in light of their radically different prevalences and intensity of infections. Host feeding preferences by vectors should be investigated. Whether true preferences or host availability to vectors influences the number of hosts infected remains open to speculation.

Vector ecology is the weakest link in our knowledge of parasite systems. The species composition of vector populations, both immature and adult, needs to be studied. Then, the life budget of ornithophilic species can be properly documented as to their seasonal abundance, distribution, and survival. Only after this can the size of the true vector population be known and the percentage of infectives be calculated.

The possibility of autumn transmission on or near the winter range was not discussed. The migratory habits of grouse, the existence of suitable vectors, the environmental conditions and the specific location of winter ranges suffer, at present, from an almost complete lack of knowledge. It would be foolhardy to speculate on transmission at higher elevations; however, should it be found that some transmission occurs as grouse slowly forage on their upward migration to wintering ranges, evidence may be forthcoming to explain why blue grouse possess higher prevalences than other birds migrating to lower latitudes.

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APPENDIX I

Non-tetraonid birds† examined for hematozoa from Comox Burn, Vancouver Island, 1974.

Order	Family	Species	No. Examined
Apodiformes	Trochilidae	*Selasphorus rufus*	28
Caprimulgiformes	Caprimulgidae	*Chordeiles minor*	10
Piciformes	Picidae	*Colaptes auratus cafer*	6
		Dendrocopus pubescens	1
		Sphyrapicus varius	1
Passeriformes	Bombycillidae	*Bombycilla cedorum*	3
	Fringillidae	*Junco hyemalis*	14
		Melospiza melodia	25
		Spinus pinus	13
		Zonotrichia leucophrys	10
	Icteridae	*Euphagus cyanocephalus*	1
		Molothrus ater	1
	Parulidae	*Dendroica coronata auduboni*	4
		D. petechia	3
		D. townsendi	1
		Geothlypis trichas	1
		Oporonis tolmei	5
		Vermivora celata	25
		Wilsonia pusilla	1
	Sylviidae	*Regulus calendula*	1
	Troglodytidae	*Troglodytes troglodytes*	3
	Turdidae	*Catharus guttatus*	1
		C. ustalatus	2
		Ixoreus naevius	1
		Myadestes townsendi	2
		Turdus migratorius	17

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APPENDIX I - continued

Non-tetraonid birds† examined for hematozoa from Comox Burn, Vancouver Island, 1974.

Order	Family	Species	No. Examined
	Tyrannidae	*Empidonax difficilis*	2
		E. t. traillii	11
		Nuttalornis borealis	5
TOTALS 4	11	29	197

† All names from the A.O.U. checklist, fifth edition (1957) and its 32nd Supplement (1973).

APPENDIX II

Seasonal abundance and distribution of Simuliidae larvae from Comox Burn, Vancouver Island, 1974.

	Number of Larvae Collected†													
	June				July					August				
Species	13	17	24	29	5	11	17	24	31	7	14	21	28	Species Total
Prosimulium dicum	3	6	1	0	0	0	0	0	0	0	0	0	0	10
P. esselbaughi	30	29	23	5	13	0	0	0	0	0	0	0	0	100
P. fulvithorax	1	0	0	0	0	0	0	0	0	0	0	0	0	1
P. travisi	42	57	43	9	6	1	0	0	0	0	0	0	0	158
Cnephia minus	0	41	10	0	0	0	0	0	2	0	0	0	0	53
Simulium aureum	0	0	0	1	1	1	1	2	36	7	3	3	3	58
S. canadense	0	0	0	4	27	5	0	11	5	31	5	1	0	89
S. hunteri	6	72	76	52	44	29	11	16	21	13	2	1	0	343
S. pugetense	0	3	0	0	2	1	0	0	0	0	0	3	0	9
S. sp.	0	1	0	0	3	0	0	0	0	0	0	0	0	4
S. sp. nov.	0	0	0	0	0	0	0	0	1	0	1	2	0	4
Weekly Total	82	209	153	71	96	37	12	29	65	51	11	10	3	829

† From 10 cm^2 ceramic tiles placed in 25 streams.

APPENDIX III

Non-simuliid hematophagous Diptera collected† from Comox Burn, Vancouver Island, 1974.

Species	Number Caught	Collection Method
Culicidae		
Aedes canadensis (Theo.)	38	aerial sweeps, feeding on man
A. varipalpus (Coq.)	14	aerial sweeps
A. stimulans (Walk.)	57	aerial sweeps
A. sp.	19	aerial sweeps
Culex territans Walk.	24	aerial sweeps, feeding on man
Anopheles punctipennis (Say)	115	aerial sweeps
	267	
Ceratopogonidae		
Culicoides obsoletus (Mg.)	12	aerial sweeps
C. crepuscularis Mall.	5	aerial sweeps
C. sp.	28	aerial sweeps
Forcipomyia tenuisquama Kieffr.	14	aerial sweeps
	59	
Hippoboscidae		
Ornithomyia fringillina Latr.	2	on passerine birds
Neolipoptena ferrisi (Bequaert)	1	aerial sweeps near deer fawn
	3	
Total	329	

† From standardized sweep net collections.

APPENDIX IV

Collection data from host-baiting experiments, 1974.

Date	Time (24 hrs)	Height (meters)	Wind† (km/hr)	Temp (°C)	Clouds†† (0-10)	Flies		Species Identification
						Blooded	Unfed	
June 14	2050-2110	6.5	2-4	15	6-7	0	0	
	2035-2055	5	1-2	17	0-1	1	1	*Cnephia minus*
17	2120-2135	3.5	1-2	16	0-1	0	0	
	0640-0700	5	0-1	14	1-2	2	1	*C. mutata*
	0730-0750	6.5	0-1	15	1-2	1	1	*C. minus*
	0820-0840	0	0-1	15	1-2	0	0	
	2100-2120	5	0-1	12	0-1	0	0	
18	2140-2155	3.5	1-2	15	0-1	0	7	*Prosimulium travisi*
	0915-0935	5	2-3	15	8-9	0	0	
	2015-2035	1.5	3-4	14	5-6	0	0	
21	2100-2120	0	3-4	13	5-6	0	0	
	1935-1955	5.0	0-1	18.5	1-2	2	0	*C. minus*
	2020-2040	3.5	1-2	14	1-2	0	0	

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APPENDIX IV - continued

Collection data from host-baiting experiments, 1974.

Date	Time (24 hrs)	Height (meters)	Wind† (km/hr)	Temp (°C)	Clouds†† (0-10)	Flies Blooded	Flies Unfed	Species Identification
24	2100-2115	1.5	3-4	12.5	1-2	0	0	
	0645-0715	6.5	2-3	9	10	3	0	*Simulium hunteri*
	0730-0750	3.5	1-2	9.5	10	0	2	*P. dicum*
	0830-0850	0	1-2	9	10	2	5	*C. minus, S. hunteri*
28	0915-0935	6.5	2-3	17	9-10	0	0	
July 1	1200-1445	3.5	1-2	15	9-10	0	25+	*S. hunteri, P. esselbaughi*
	0715-0735	5.0	0	11	9-10	1	1	*S. aureum*
	0800-0820	3.5	0	12	9-10	1	1	*S. hunteri, P. travisi*
	0900-0920	6.5	0-1	14.5	8-9	4	4	*S. hunteri, P. travisi*
4	1000-1020	0	0-1	17	8-9	0	0	
	2000-2020	5.0	0	19.5	9	0	32	*S. hunteri*
	2045-2105	1.5	0	19	10	0	0	

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APPENDIX IV - continued

Collection data from host-baiting experiments, 1974.

Date	Time (24 hrs)	Height (meters)	Wind† (km/hr)	Temp (°C)	Clouds†† (0-10)	Flies Blooded	Flies Unfed	Species Identification
8	2130-2150	5.0	0-1	16	10	3	0	*S. hunteri*
	2015-2035	3.5	3-5	14	8-9	0	2	*C. minus, S. hunteri*
	2100-2020	3.5	0-1	12	9	2	0	*S. aureum, S. hunteri*
22	2000-2020	3.5	0-1	17.5	8	5	0	*S. hunteri*
23	2055-2115	3.5	0-1	15	6-7	1	0	*S. aureum*
	1915-1935	0	0-1	17	4	0	0	
	2000-2020	3.5	2-3	16.5	4	2	0	*S. aureum*
24	2040-2100	6.5	0-1	13	3	1	0	*S.* sp.
	1935-1955	3.5	1-2	14.5	1-2	1	2	*S. aureum, C. minus*
29	2015-2035	5	1-2	13	2	4	0	*C. minus, S. hunteri*
August 2	2000-2020	0	0-1	15	1	0	0	
	0655-0715	6.5	0-1	10	0	4	2	*S. canadense, S. hunteri*

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APPENDIX IV - continued

Collection data from host-baiting experiments, 1974.

Date	Time (24 hrs)	Height (meters)	Wind† (km/hr)	Temp (°C)	Clouds†† (0-10)	Flies		Species Identification
						Blooded	Unfed	
	0740-0800	5	1-2	22	0	0	3	*S. aureum, S. hunteri*
8	0830-0850	1.5	1-2	14	0	0	1	
	1930-1950	3.5	5	20	3	0	0	
12	2020-2040	0	1-2	12	4	0	0	
	1930-1950	5	0	17	3	5	0	*C.* sp.
13	2010-2030	1.5	5	17	4	0	0	
	1900-1920	0	0	19	3	0	0	
	1945-2005	3.5	1-2	15	1	2	0	*S.* sp.
15	2035-2055	5	1-2	12	1	0	0	
	1510-1530	0	0	25	0	0	0	
	1600-1620	6.5	1-2	23	1	0	0	
16	1645-1705	1.5	1-2	22	1	0	0	

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APPENDIX IV - continued

Collection data from host-baiting experiments, 1974.

Date	Time (24 hrs)	Height (meters)	Wind† (km/hr)	Temp (°C)	Clouds†† (0-10)	Flies Blooded	Flies Unfed	Species Identification
	2000-2020	5	1-2	15	2	2	6	*S. hunteri*
17	2045-2105	3.5	2-3	12	2	0	0	
	1905-1925	0	3-4	16	10	0	0	
22	1945-2005	1.5	3-4	14	10	0	0	
TOTALS	53					49	96	Number of Species = 7

†Relative velocity adjusted to: 1 = 0.62 km/hr (1 mph); 3 = 3.2 km/hr (5 mph); 5 = 6.25 km/hr (10 mph).

††Percent cloud cover: 1 = 10%, 2 = 20%, etc.

APPENDIX V

Frequency of multiple infections in Blue Grouse from Comox Burn, Vancouver Island, 1973 and 1974.

	Double						Triple				Quadruple
	L†-H	*L-T*	*L*-Mf	*H-T*	*H*-Mf	*T*-Mf	*L-H-T*	*L-H*-Mf	*L-T*-Mf	*H-T*-Mf	*L-T-H*-Mf
1973 N = 381											
No. Infected	40	16	3	9	0	2	93	21	10	4	122
Frequency (%)	6	3	1	2	0	0.1	11	3	1	1	12
Expected (%)	67	58	37	52	34	29	45	29	25	22	19
Total			70						128		122
1974 N = 307											
No. Infected	56	20	8	0	1	0	23	8	4	0	3
Frequency (%)	18	7	3	0	0.1	0	6	2	1	0	1
Expected (%)	22	12	6	6	3	1	4	2	1	0	0
Total			85						35		3

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APPENDIX V - continued

Frequency of multiple infections in Blue Grouse from Comox Burn, Vancouver Island, 1973 and 1974.

	Double						Triple				Quadruple
	L†-*H*	*L*-*T*	*L*-Mf	*H*-*T*	*H*-Mf	*T*-Mf	*L*-*H*-*T*	*L*-*H*-Mf	*L*-*T*-Mf	*H*-*T*-Mf	*L*-*T*-*H*-Mf
Total N = 688											
No. Infected	96	36	11	9	1	2	116	29	14	4	125
Frequency (%)	10	4	2	1	0.1	0.1	9	3	0.1	1	9
Expected (%)	45	36	21	26	15	12	20	12	10	7	5
Total	155						163				125

†*L* = *Leucocytozoon bonasae*, *H* = *Haemoproteus canachites*, *T* = *Trypanosoma avium*, Mf = Microfilaria.

APPENDIX VI

Correlation of prevalences and intensities of avian hematozoa in all age and sex classes of Blue Grouse from Comox Burn, Vancouver Island, 1973 and 1974.

	$\bar{x}$ Prevalence ($\pm$S.E.)	$\bar{x}$ Intensity ($\pm$S.E.)	Correlation† Coefficient
Leucocytozoon bonasae	0.86	15.1	0.145
	(0.16 $\bar{x}$)	(12.4)	
Haemoproteus canachites	0.63	44.8	0.139
	(0.31)	(37.3)	
Trypanosoma avium	0.49	2.0	0.878*
	(0.28)	(0.85)	
Microfilaria	0.297	2.01	0.831*
	(0.22)	(0.92)	

†Prevalence and intensity values are not randomly distributed.

*$P < 0.05$.